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MOLLUSCAN TAXA AND BIBLIOGRAPHIES OF WILLIAM JAMES CLENCH AND RUTH DIXON TURNER

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SPECIAL PUBLICATIONS.

1. Whittington, H. B., and W. D. I. Rolfe (eds.), 1963 Phylogeny and Evolution of Crustacea. 192 pp.
2. Turner, R. D., 1966. A Survey and illustrated Catalogue of the Teredinidea (Mollusca: Bivalvia). 265 pp.
3. Sprinkle, J., 1973. Morphology and Evolution of Blastozoan Echinoderms. 284 pp.
4. Eaton, R. J., 1974. A Flora of Concord from Thoreau's Time to the Present Day. 236 pp.
5. Rhodin, A. G. J., and K. Miyata (eds.), 1983. Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams. 725 pp.
6. Angelo, R., 1990. Concord Area Trees and Shrubs. 118 pp.

Other Publications.

Bigelow, H. B., and W. C. Schroeder, 1953. Fishes of the Gulf of Maine. Reprinted 1964.

Brues, C.T., A. L. Melander, and F. M. Carpenter, 1954. Classification of Insects. (*Bulletin of the M. C. Z.*, Vol. 108.) Reprinted 1971.

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Lyman, C. P., and A. R. Dawe (eds.), 1960. Proceedings of the First International Symposium on Natural Mammalian Hibernation. (*Bulletin of the M. C. Z.*, Vol. 124.)

Orinthological Gazetteers of the Neotropics (1975–).

Peter's Check-list of Birds of the World, vols. 1–16.

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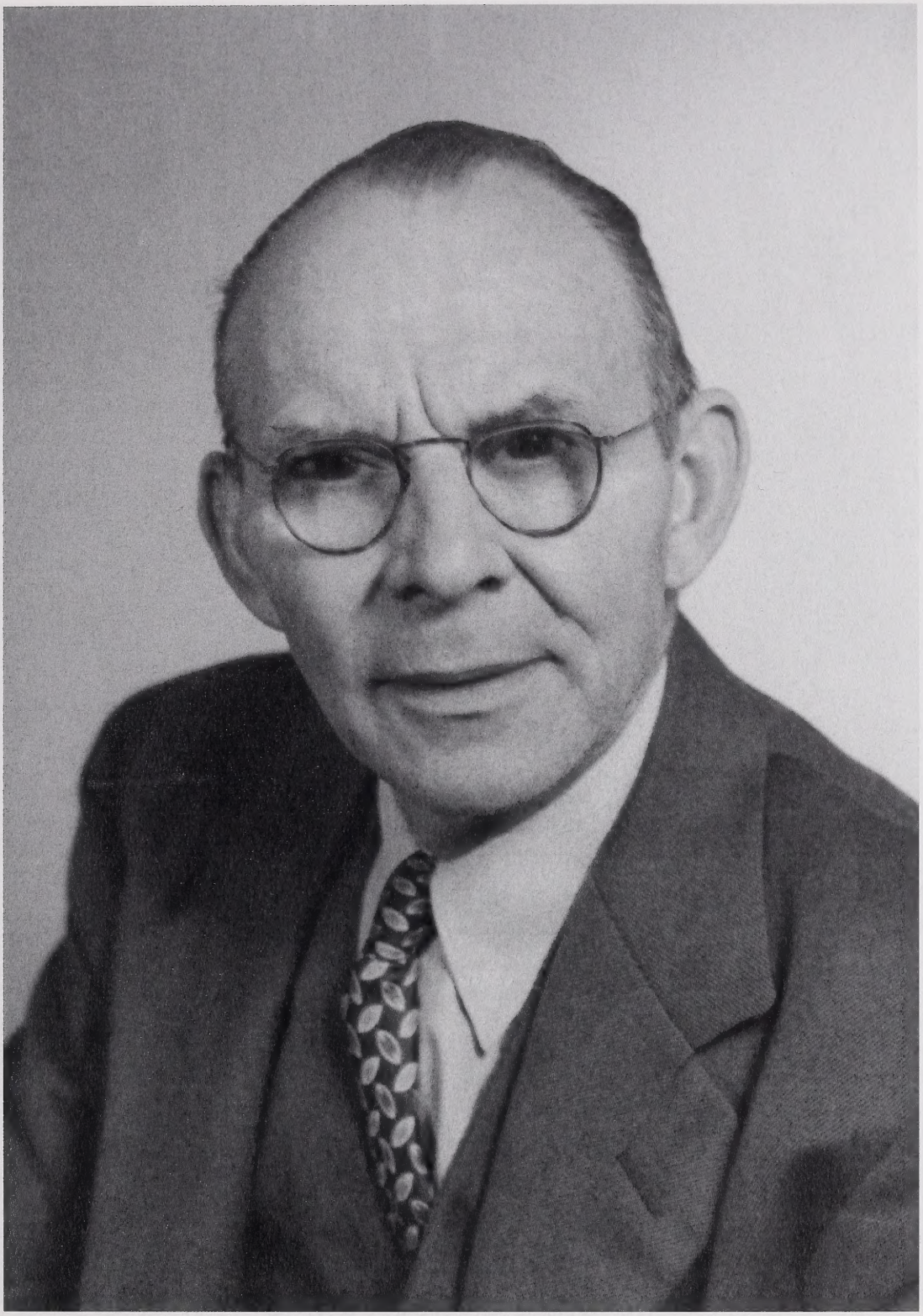

William J. Clench
Taken in 1953.
A number of other pictures of Clench appeared
in Abbot (1984).

Ruth D. Turner
Taken in the Department of Mollusks, 1957.
A later portrait can be found in Mann (2000).

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RICHARD I. JOHNSON[1]

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ABSTRACT. Between 1924 and 2002, William J. Clench (1897–1984) and Ruth D. Turner (1914–2000) introduced over 500 molluscan taxa, almost 70 of them jointly. All of their taxa are included in a single list, giving the original reference, type locality, and location of the type specimens. Their bibliographies are separate.

INTRODUCTION

Almost immediately after the death of William J. Clench in 1984, Professor Ruth D. Turner began a memorial to him, which was also to include a list of his publications and new taxa. This should have been a simple task since she had available Clench's own running list of both, which also indicated the catalog number of most of the new species and subspecies he had described. Some 15 years later at the time of her own death in 2000, only the bibliography had been made available. She had, however, brought all of his papers together, and had prepared an elaborate folder with the title page of each mounted as if she had intended these for publication.

The Museum of Comparative Zoology is just over 140 years old, and the mollusk collection dates back to the 1830s through the collection of the Boston Society of Natural History. Thus, Clench (1897–1984) and Turner (1914–2000), who were individually or collectively associated with the Museum for nearly 75 years (i.e., 1926–2000), or more than half of its existence, had a remarkable institutional memory of the Museum and the mollusk collection. Because their lives were so intertwined for so long in the history of the department, and because they did much joint work, it seemed appropriate to include both in a single study. Complete bibliographies are included for each, but there is a single list of described taxa. Over 400 were introduced by Clench, an occasional few by Clench and others, 68 by Clench and Turner, and only 34 by Turner alone or with authors than Clench.

Turner's work as a researcher slowed prior to her health problems beginning in about 1995, and she was severely disabled in the last several months of her life. She left an important manuscript on the pholadacean bivalve genera, *Xylophaga, Xyloredo,* and *Xylopholas,* that she had been preparing for a number of years through

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active support by the Office of Naval Research (ONR). Ms. Helene Ferranti, a long-time coworker and associate of Turner, prepared the work for publication (Turner, 2002). The seven new species introduced are included here. *A Projected Key to the Gastropoda of the Woods Hole, Massachusetts Area,* begun by Turner several decades ago with the collaboration of several others, became so elaborate that it was never made ready for publication. An additional work alluded to by Mann (2000: 8) was also not found in a publishable state.

BIOGRAPHICAL REFERENCES AND OBITUARIES

ABBOTT, R. T. 1973. Clench, William J(ames), p. 234. [In] American Malacologists. Falls Church, Maryland: American Malacologists.

———. 1984. A farewell to Bill Clench. The Nautilus, **98**(2): 55–58.

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TURNER, R. D. 1985. William J. Clench October 24, 1897–February 22, 1984. Malacological Review, **18**(December): 123–124.

———. 2002. On the subfamily Xylophagainae (Family Pholadidae, Bivalvia, Mollusca). Bulletin of the Museum of Comparative Zoology, **157**(4): 223–308; 38 pls.

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METHODS AND ACKNOWLEDGMENTS

A few species were described from unique specimens in the possession of others. The remainder are represented in the Museum of Comparative Zoology by the holotype or paratypes, with the exception of *Cepolis garciana, Cerion disforme nodali, Emoda blanesi, Helicina holguinensis,* and *Jeanneretia parraiana carinata,* all described by Clench and Aguayo in 1953, paratypes of which are mentioned as from the Museo Poey, Havana, Cuba. They were never received. Present efforts have failed to secure them.

If the holotypes are in the Museum of Comparative Zoology, paratypes when present there or elsewhere are not always listed. This is especially true among the *Cerion,* where the paratype lots often consist of staggering numbers.

The locality data here are as originally presented. Name changes, especially in Africa and Oceanica, have been so frequent that it has been deemed best to let those who might use this list make the changes as required.

The following abbreviations have been used in the list of taxa.

AMNH	American Museum of Natural History, New York, New York
ANSP	Academy of Natural Sciences of Philadelphia, Pennsylvania
Australian Museum	Sydney, New South Wales
Bishop Museum	Bernice P. Bishop Museum, Honolulu, Hawaii
Carnegie Museum	Pittsburgh, Pennsylvania
Florida Museum of Natural History	Gainsville, Florida
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts
MRAC	Musée Royal de l'Afrique Centrale, Tervueren
Museo Poey	Havana, Cuba
UMMZ	Museum of Zoology, University of Michigan, Ann Arbor, Michigan
ZMB	Zoologischen Museum, Berlin

Thanks are extended to the following for information regarding the type specimens of some of the species mentioned in this paper. Mr. John Slapcinsky, Florida Museum of Natural History, University of Florida, Gainesville, Florida; Dr. Daniel L. Graf, Museum of Zoology, University of Michigan, Ann Arbor, Michigan; Dr. Didier Vandenspiegal, Musée Royal de l'Afrique Centrale, Tervuren, Belgium; Dr. J. L. Van Goethem, Institut royal des Sciences naturelles de Belgique, Bruxelles; Dr. Bernhard Hausdorf, Zoologisches Museum der Universitaet Hamburg, Germany; Dr. Ole S. Tendal, Zoologisk Museum, Kobenhavns Universitet, Denmark; and Dr. John Stanisic, Queensland South, Brisbane, Australia. Dr. Diarmaid O'Foighil, Museum of Zoology, University of Michigan, kindly supplied a paratype of a *Physa* described by Clench not represented in the MCZ.

Ms. Mary Sears, Ms. Susan DeSanctis, and Mr. Ronnie Broadfoot of the library of the Museum of Comparative Zoology and Dr. Robert Toll, Dean of the College of Natural Sciences and Mathematics of the University of Central Arkansas, Conway, Arkansas, each helped to locate difficult references.

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TAXONOMIC LIST AND PUBLICATIONS

Molluscan Taxa Introduced by William J. Clench and Ruth D. Turner with Their Original References, Type Localities, and Locations of Type Specimens

Abaconia (subgenus) Clench 1938, Mem. Soc. Cubana Hist. Nat., **12:** 321 (type species, *Leptinaria* [*Abaconia*] *naufraga* Clench 1938, original designation). [A synonym of *Litiopa*, teste Clench.]

abbotti Clench, *Cerion* (*Strophiops*) *utowana* 1961, Occas. Pap. Mollusks, **2:** 251, pl. 43, fig. 4 (Long Island, South Caicos Islands, Bahamas); holotype USNM 610285; paratypes MCZ 189954.

abbotti Clench, *Conus regius* 1942, Johnsonia, **1**(6): 6, pl. 4, figs. 2, 3 (Arthurstown, Cat Island, Bahamas); holotype MCZ 145274.

abbotti Clench & Turner, *Opalia* (*Opalia*) 1952, Johnsonia, **2:** 348, pl. 171 (*Atlantis* Sta. 3374, 20°45′N, 75°19′W, Puerto Tanamo, Cuba, 300 fth.); holotype MCZ 184511.

abbotti Clench & Turner, *Taheitia arcasiana* 1948, Occas. Pap. Mollusks, **1**(13): 187, pl. 22, fig. 3, pl. 23, fig. 2, pl. 24, fig. 1 (first gully from west, north side of Somoloma Hill, 9 mi. S of Lautoka, NW Viti Levu, Fiji Islands); holotype MCZ 179578.

achatinus Clench, *Liguus fasciatus* 1934, Occas. Pap. Boston Soc. Nat. Hist., **8:** 107, fig. 1 (Los Arroyos, Holguín, Oriente, Cuba); holotype MCZ 58803.

acklinsensis Clench, *Eutrochatella* 1963, Bull. Mus. Comp. Zool., **128:** 398, pl. 3, fig. 4 (inland from Cornucopia, Acklins, Island, Bahamas); holotype USNM 390633, paratype MCZ 225315.

Acrostylus (subgenus) Clench 1935, Nautilus, **48:** 126 (type species, *Placostylus* [*Acrostylus*] *acutus* Clench 1935, original designation).

acutus Clench, *Placostylus* (*Acrostylus*) 1935, Nautilus, **48:** 126, pl. 7, fig. 6 (Wanderer Bay, Guadalcanal, Solomon Islands); holotype MCZ 93953.

aequatorialis Bequaert & Clench, *Archachatina* (*Megachatinops*) *gaboonensis* 1936, Rev. Zool. Bot. Afr., **29**(1): 90, pl. 1, fig. 4 (Kunungu, near Bolobo, Belgian Congo); holotype MRAC 339. 640; paratype MCZ 103894.

africana Clench, *Rhinomelania* 1929, Bull. Mus. Comp. Zool., **69:** 119, text fig. 1 (Kribi, Cameroon); holotype MCZ 15794.

Afroditropis (genus) Bequaert & Clench 1936, Rev. Zool. Bot. Afr., **29**(1): 102 (type species, *Afroditropis strongi* Bequaert & Clench, 1936, original designation).

afromontana Bequaert & Clench *Achatina*, Rev. Zool. Bot., **24**(3): 269, pl. 1, figs. 2, 12 (Western Ankole, Uganda); holotype MCZ 77208.

agassizi Clench & Aguayo, *Metula* 1941, Mem. Soc. Cubana Hist. Nat., **15**(2): 179, pl. 14, fig. 4 (*Atlantis* Sta. 3443, 23°22′N, 79°53′W, off Vagua la Grande, Cuba, 325 fth.); holotype MCZ 135248.

agglutinans Bequaert & Clench, *Potadoma* 1941, Bull. Mus. Comp. Zool., **88**(1): 10, pl. 1, figs. 1–8,

10 (estuary of the Congo River, Kala-Kala, near Matadi, Belgian Congo); holotype MCZ 112267.

aguayoi Clench, *Bathyaurinia* 1940, Mem. Soc. Cubana Hist. Nat., **14**(3): 241, pl. 42, fig. 4, text fig. 1 (*Atlantis* Sta. 3783, 30°3′N, 78°37′W; 164 mi. off St. Augustine, Florida; 425–330 fth.); holotype MCZ 111858.

aguayoi Torre & Clench, *Cerion* 1932, Nautilus, **45:** 89, pl. 6, figs. 6, 7 (road to Caletones about 6 km W Gibana, Oriente, Cuba); holotype MCZ 47902.

aguayoi Clench, *Cerithium* 1934 [in] Johnson, Proc. Boston Soc. Nat. Hist., **40:** 110 (new name for *Cerithium varicosum* Sowerby 1834, non Defrance 1817; Valenciennes 1832; Anton 1839; Eudes 1842.

aguayoi Clench, *Liguus fasciatus* 1934, Occas. Pap. Boston Soc. Nat. Hist., **8:** 109, pl. 7, fig. 2 (Punta Roja, Holguín, Oriente, Cuba); holotype MCZ 76696.

aguayoi Clench & Pérez Farfante, *Murex* (*Murex*) 1945, Johnsonia, **1**(17): 15, pl. 8, figs. 1–3 (*Atlantis* Sta. 3415, 22°51′30″N, 78°55′30″W, off Punta, Alegre, Camagüey, Cuba, 210 fth.); holotype MCZ 147286.

alberti Clench & Aguayo, *Cerion* 1949, Torreia (Univ. Havana), (14): 3, pl. 1, figs. 1–6 (Punta de "El Fuerte," Entrada de la Bahiá de Banes, Peninsula de Ramon, Antilla, Cuba); holotype MCZ 166621, paratypes Museo Poey 4159.

alberti Clench & Aguayo, *Chondropoma* 1948, Rev. Soc. Malacól. "Carlos de la Torre," **6**(2): 53, text fig. (0.5 mi. S of Cavo Lucrecia, Banes, Oriente, Cuba); holotype Museo Poey 12974, paratypes MCZ 175753.

albertisi Clench, *Westralunio* 1957, Breviora, (76): 3, fig. 2 (inland from Daru, Western Division, Papua, New Guinea); holotype MCZ 212908.

Alleghenya Clench & Boss, 1967, Nautilus, **80:** 101 (new name for *Madalia* of authors non Haldeman 1840).

alleni Clench & Aguayo, *Odontosagda* 1932, Proc. N. Engl. Zool. Club, **13:** 36 (Petionville, Haiti); holotype MCZ 23425.

almiranta Clench, *Placostylus* (*Proaspastas*) 1941, Am. Mus. Novit., (1129): 14, fig. 7 (10 mi. inland from Su'u Malaita Island, Solomon Islands, 1,500 ft.); holotype AMNH 79009; paratype MCZ 93001.

altenai Turner, *Xylopholas* 1972, Basteria, **36**(2–5): 99, figs. 1–12 (R/V *Gerda* Sta. 66, 25°25′N, 79°59′W, about 13 mi. SE Fowey Rocks, Florida, 200 fth.); holotype MCZ 279315.

amoi Cooke & Clench, *Succinea* 1945, Occas. Pap. B. P. Bishop Mus., **18**(8): 135, fig. 3 (Papenoo Valley, Mt. Orofena, Tahiti, Society Islands, 4,000 ft.); holotype Bishop Museum 145634, paratype MCZ 146393.

amplior Bequaert & Clench, *Archachatima* (*Megachatinops*) *camerunensis* 1936, Rev. Zool. Bot. Afr., **29**(1): 89, pl. 1, fig. 12 (Libreville, French Congo); holotype MCZ 59323.

andersoni Cooke & Clench, *Rapanella* 1943, Occas. Pap. B. P. Bishop Mus., **17**(20): 254, fig. 3 (Maitua, below Mt. Mangaoa, Rapa Island, Central Pacific); holotype Bishop Museum 189005, paratypes MCZ 140596.

angelae Clench & Aguayo, *Liguus fasciatus* 1934, Occas. Pap. Boston Soc. Nat. Hist., **8:** 110, pl. 7, fig. 3 (Punta Roja, Holguín, Oriente, Cuba); holotype MCZ 76698.

aopta Clench & Archer, *Helicostyla* (*Calocochlea*) 1933, Pap. Mich. Acad. Sci. Arts Lett., **17:** 542, pl. 57, fig. 3 (between Puerto Galera and San Teodoro, Mindoro, Philippines); holotype MCZ 81354.

arangoi Clench & Aguayo, *Jeanneretia parraiana* 1951, Rev. Soc. Malacól. "Carlos de la Torre," **7:** 84, pl. 13, figs. 16, 18 (Sitio del Infierno, Viñales, Cuba); holotype Museo Poey 15079, paratypes MCZ 127393, 105218, 114958.

archeri Clench, *Helicostyla subcarinata* 1936, Nautilus, **49:** 140, pl. 8, fig. 5 (Tres Reyes Islands, SW coast of Marinduque, Philippine Islands); holotype MCZ 96474.

archeri Clench, *Liguus fasciatus* 1934, Occas. Pap. Boston Soc. Nat. Hist., **8:** 106, pl. 7, fig. 5 (Mogote de Ramon Millo, Viñales, Pinar del Rio, Cuba); holotype MCZ 80901.

arenarius Clench & Pérez Farfante, *Murex florifer* 1945, Johnsonia, **1**(17): 34, pl. 19, figs. 1–3 (Sanibel Island, Florida); holotype MCZ 149854.

argo Clench & Pérez Farfante, *Murex* (*Chicoreus*) 1945, Johnsonia, **1**(17): 31, pl. 17, fig. 1 (new name for *imbricatus* Higgins & Marrat, 1877; non Brocchi 1814, Risso 1826, Nardo 1847).

ariomus Clench & Pérez Farfante, *Murex* (*Pterynotus*) 1945, Johnsonia, **1**(17): 39, pl. 20, figs. 5–6 (off Hollywood, Florida, 50–60 fth.); holotype MCZ 164734.

ariomus Clench, *Plysa pomilia* 1925, Occas. Pap. Mus. Zool., Univ. Mich., (161): 2, pl. 1, fig. 2 (Gastonburg, Wilcox Co., Alabama); holotype UMMZ 32231; paratypes MCZ 55658.

ariomus Clench & Aguayo, *Potamopyrgus coronatus* 1937, Mem. Soc. Cubana Hist. Nat., **11:** 68, pl. 7, fig. 10 (Lake Miragoane, Haiti, 2 mi. S of Miragoane, Haiti); holotype MCZ 108818.

armouri Clench, *Ceron* (*Strophiops*) 1933, Proc. N. Engl. Zool. Club, **13:** 96, pl. 1, fig. 4 (S coast of Mariguana Island, Bahamas); holotype MCZ 101163.

armouri Clench, *Chondropoma beatensis* 1932, Proc. N. Engl. Zool. Club, **12:** 106 (Beata Island, Santo Domingo); holotype MCZ 81495.

atalanta Clench, *Chloritis* (*Sulcobasis*) 1933, Nautilus, **47:** 23, pl. 3, figs. 9, 10 (New Hanover Island, Bismark Archipelago); holotype MCZ 59844.

atalanta Bequaert & Clench, *Forbesopomus* 1937, Proc. N. Engl. Zool. Club, **17:** 54, pl. 2, figs. 1–7 (Lake Lanao, Misamis, Mindoro, Philippine Islands); holotype MCZ 74465.

atalanta Clench, *Papuina williamsi* 1936, Nautilus, **50:** 54 (Omarakana, North Central Kiriwina Island, Trobriand Islands); holotype MCZ 111151.

athearni Clench & Turner, *Goniobasis* 1956, Bull.

Fla. State Mus., **1**(3): 131, pl. 2, fig. 6 (Chipola River, 2.5 mi. SE of Chason, Calhoun Co., Florida); holotype MCZ 190102.

atkinsi Torre & Clench, *Urocoptis livida* 1930, Nautilus, **44:** 15, pl. 2, figs. 5, 6 (Vilches Potrero, Central Soledad, Cienfuegos, Cuba); holotype MCZ 59108.

atlantica Clench, *Casmaria* 1944, Johnsonia, **1**(16): 2, pl. 1, figs. 1, 2 (Puerto Sosúa, Hispaniola); holotype MCZ 57284.

atlanticus Macdonald & Clench, *Bigelowia* 1934, Occas. Pap. Boston Soc. Nat. Hist., **8:** 145, text figs. 1–9 (37°N, 67°12′W, North Atlantic); holotype MCZ 98971.

atlanticus Clench & Aguayo, *Ficus* 1940, Mem. Soc. Cubana Hist. Nat., **14**(1): 85, pl. 14, fig. 1 (*Hassler* Voyage, 11°49′S, 37°10′W, off Sao Salvador, Bahía Prov., Brasil 1872, 45 fth.); holotype MCZ 104657.

atlantis Clench & Aguayo *Calliostoma* (*Calliostoma*) 1940, Mem. Soc. Cubana Hist. Nat., **14:** 81, pl. 15, fig. 4 (*Atlantis* Sta. 3306, 23°4′30″N; 82°37′W, off Mariel, Pinar del Rio Prov., Cuba, 330 fth.); holotype MCZ 135164.

atlantis Clench & Aguayo, *Columbarium* 1938 (*Atlantis* Sta. 2999, 23°10′N, 81°29′W, off Matánzas, Cuba, 421 fth.); holotype MCZ 135004.

atlantis Clench & Pérez Farfante, *Murex* (*Bathymurex*) 1945, Johnsonia, **1**(17): 41, pl. 21, figs. 3–5 (*Atlantis* Sta. 3333, 22°13′N, 81°11′W, Bahía de Conchinos, Santa Clara, Cuba, 190–200 fth.); holotype MCZ 164684.

atlantis Clench & Turner, *Nystiella* 1952, Johnsonia, **2:** 343, pl. 168 (*Atlantis* Sta. 3330, 22°9′N, 81°10′W, Bahía de Cochinos, Cuba, 230–265 fth.); holotype MCZ 187988.

atlantis Clench, *Scaphella* (*Anrinia*) 1946, Johnsonia, **2:** 53, pl. 29, fig. 5 (*Atlantis* Sta. 3415, 22°51′N, 78°55′30″W, off Punta Alegre, Camagüez, Cuba, 210 fth.); holotype MCZ 135263.

augusti Clench & Aguayo, *Opisthosiphon caroli* 1949, Rev. Soc. Malacól. "Carlos de la Torre," **6:** 90, pl. 2, fig. 2 (Finca Flores, cerca del Mir, Holguín, Cuba); holotype Museo Poey 12352, paratypes MCZ 174284.

aurantius Clench, *Liguus crenatus* 1929, Nautilus, **43:** 19 (Hammock #408[#5] Pincecrest Region, Central Everglades, Florida); holotype MCZ 84624.

Auriniopsis (genus) Clench, 1953, Johnsonia, **2:** 378 (type species, *Scaphella kieneri* Clench 1946, original designation).

bahamensis Clench, *Byssanodonta* 1938, Bull. Mus. Comp. Zool., **80**(14): 535, pl. 2, fig. 6 (0.5 mi. due E of Arthurs Town, Cat Island, Bahamas); holotype MCZ 107726.

bahamensis Clench *Ferrissia* (*Laevapex*) 1938, Mem. Soc. Cubana Hist. Nat., **12:** 318, pl. 24, fig. 23 (Eight Mile Road, Grand Bahama Island, Bahamas); holotype MCZ 116723.

bahamensis Clench & Turner *Truncatella bilabiata* Johnsonia, **2:** 155, pl. 67, figs. 1–5 (Northwest Point, Little Inagua Island, Bahamas); holotype MCZ 158794.

banesense Clench & Aguayo, *Cerion* 1949, Torreia (Univ. Havana), (14): 7, pl. 1, figs. 13–15 (Al Este de la Bahía de Samá, Banes, Oreinte, Cuba); holotype MCZ 166623, paratypes Museo Poey 9420.

Bankiinae (subfamily) Turner, 1966, A Survey and Illustrated Catalogue of the Teredinidae, p. 78.

Bankiopsis (subgenus) Clench & Turner, 1946, Johnsonia, **2**(19): 16 (type species, *Bankia caribbea* Clench & Turner 1946, original designation).

barberi Clench, *Physa* 1925, Occas. Pap. Mus. Zool., Univ. Mich., (164): 2, pl. 1, figs. 1–3 (canal embankment, West Palm Beach, Florida); holotype UMMZ 32540, paratypes MZUM 32451; Clench collection 2012 [not located in MCZ].

barbouri Clench, *Archegocoptis* 1935, Proc. Boston Soc. Nat. Hist., **41:** 5, pl. 1, figs. B–F (Tardieu Mt., La Hotte, Haiti, 3,000 ft.); holotype MCZ 108593.

barbouri Clench, *Brachypodella* (*Anguliceruix*) 1935, Proc. Boston Soc. Nat. Hist., **41:** 10, pl. 1, fig. K (La Visite, La Selle Range, Haiti); holotype MCZ 108587.

barbouri Clench & Aguayo, *Calliostoma* (*Astele*) 1946, Rev. Soc. Malacól. "Carlos de la Torre," **4:** 89, text fig. (Arenas de la Charrera, Havana [Santa Fé], Cuba, 3–15 fth.); holotype MCZ 178128, paratype Museo Poey 11602.

barbouri Clench, *Cerion* (*Strophiops*) 1933, Proc. N. Engl. Zool. Club, **13:** 95, pl. 1, fig. 5 (S coast of Mariaguana Island, Bahamas); holotype MCZ 101159.

barbouri Clench, *Eutrochatella calida,* Proc. N. Engl. Zool. Club, **13:** 82, pl. 1, fig. 13 (SW sides of Mariaguana Island, Bahamas); holotype MCZ 101185.

barbouri Clench, *Liguus crenatus* 1929, Nautilus, **43:** 18 (Hammock #21, Pinecrest Region, Central Everglades, Florida); holotype MCZ 84527.

barbouri Clench & Aguayo, *Oocorys* 1939, Mem. Soc. Cubana Hist. Nat., **13**(3): 193, pl. 29, fig. 2 (*Atlantis* Sta. 2987, 23°22′N, 79°53′W, off Sagua la Grande, Cuba, 280–300 fth.); holotype MCZ 135055.

barbouri Clench, *Opisthosiphon bahamense* 1933, Proc. N. Engl. Zool. Club, **13:** 84, pl. 1, fig. 14 (back of Victoria Hill Settlement, Watling Island, Bahamas); holotype MCZ 101180.

barbouri Torre & Clench, *Urocoptis livida* 1930, Nautilus, **44:** 15, pl. 2, figs. 7–9 (La Portuguesa, Central Soledad, Cienfuegos, Cuba); holotype MCZ 59111.

bardwelli Clench, *Hydridella* (*Hydridella*) 1934, J. Conch., **20**(3): 89, pl. 2, figs. 1–5 (lower reaches of Glenelg River, Kimberly Division, Western Australia); holotype MCZ 41999, paratypes MCZ 42000.

bardwelli Clench & McLean, *Macrocallista* (*Paradione*) 1936, J. Conch., **20**(7): 201, text fig. (Broome, Western Australia); holotype MCZ 92135.

bartletti Clench & Aguayo, *Columbarium* 1940, Mem. Soc. Cubana Hist. Nat., **14**(1): 86, pl. 14, fig.

3 (*Blake* Sta. 9, 18°12′N, 78°20′W, off Homer's Cove, Westmoreland, Jamaica, 254 fth.); holotype MCZ 104729.

bartschi Clench & Archer, *Helicostyla* (*Calochlea*) 1933, Pap. Mich. Acad. Sci. Arts Lett., **17:** 541, pl. 57, fig. 2 (Anduyanan Palúan, Mindoro, Philippines); holotype MCZ 81365.

Bathyaurinia (genus) Clench & Aguayo, 1940, Mem. Soc. Cubana Hist. Nat., **14**(1): 92 (type species *Aurinia torrei* Pilsbry 1937, original designation).

Bathymurex (subgenus) Clench & Pérez Farfante, 1945, Johnsonia, **1**(17): 41 (*Murex* [*Bathymurex*] *atlantis* Clench & Perez 1945, original designation).

bayeri Turner, *Xylophaga* 2002, Bull. Mus. Comp. Zool., **157**(4): 260, pls. 30, 31. (26°4′N; 80°4′W, 3.2 mi. off Fort Lauderdale, Florida, 152.4 m); holotype MCZ 316738, paratype MCZ 316739.

beatensis Clench, *Chondropoma* (*Chondropomium*) 1932, Proc. N. Engl. Zool. Club, **12:** 106 (Beata Island, Santo Domingo); holotype MCZ 81493, paratypes MCZ 81494.

beattyi Clench, *Brachypodella* (*Brachypodella*) 1951, J. Conchy., **90:** 275, fig. 3 (Mona Island, Puerto Rico); holotype MCZ 171015.

beattyi Clench, *Drymaeus elongatus* 1951, J. Conchy., **90:** 273, figs. 4–6 (Mona Island, Puerto Rico); holotype MCZ 171032.

beattyi Clench, *Plagioptycha euclasta* 1940, Mem. Soc. Cubana Hist. Nat., **14**(3): 244, pl. 42, fig. 3 (Mt. Eagle, St. Croix, Virgin Islands); holotype MCZ 110342.

bellonensis Clench, *Eustomopsis* 1958, Natural History of Rennell Island, British Solomon Islands, Copenhagen, Denmark, **2:** 196, pl. 19, figs. 1–3, text fig. 2 (Bellona Island, Solomon Islands); holotype AMNH 66430, paratype MCZ 92958.

bencomoi Clench, *Urocoptis* (*Autocoptis*) 1935, Proc. Boston Soc. Nat. Hist., **41:** 3, pl. 2, fig. B (vicinity of Port au Prince, Haiti); holotype MCZ 108508.

bequaerti Clench & Miller *Ashmunella* 1966, Breviora, (244): 1, pl. 1, text figs. 1, 2 (Goat Cave Canyon, near Buffalo Trail Boy Scout Camp, NE slope of Black Mt., Davis Mts., Jeff Davis Co., Texas); holotype MCZ 260274.

bequaerti Torre & Clench, *Cerion aguayoi* 1932, Nautilus, **45:** 91, pl. 6, fig. 8 (dunes at Lucrecia lighthouse, near Banes, Oriente, Cuba); holotype MCZ 86177, paratypes MCZ 86176.

bequaerti Clench & Turner, *Megalacron* 1964, J. Malacol. Soc. Aust., (8): 48, pl. 9, fig. 10 (new name for *Helix trochus* Quoy & Gaimard 1832, non Müller 1821 and *Helix trochoides* Deshayes 1838, non Poiret 1789, Gmelin 1790).

bequaerti Clench & Pérez Farfante, *Murex* (*Pteropurpura*) 1945, Johnsonia, (17): 40, pl. 21, figs. 1, 2 (off Delray, Florida, 80 fth.); holotype Florida Museum of Natural History (UF) 11986.

berevoensis Clench & Archer, *Achatuia panthera* 1930, Nautilus, **43**(3): 85 (forest between Mahabo and Berevo, cotype [lectotype] 31078; Berevo, cotype [paralectotype] MCZ 31077; 10 mi. S of Berevo, elevation 850–900 ft., cotype [paralectotype] MCZ 31079, all Madagascar); lectotype MCZ 31078 selected by J. C. Bequaert, 1950, Bull. Mus. Comp. Zool., **105**(1): 107, pl. 5, fig. 3.

bermudensis Clench, *Conus* 1942, Johnsonia, **1**(6): 34, pl. 13, fig. 4 (Dyer Island, Bermuda); holotype MCZ 141965.

bermudezi Clench & Aguayo, *Aurinia* 1940, Mem. Soc. Cubana Hist. Nat., **14**(1): 89, pl. 16, fig. 3 (*Atlantis* Sta. 2962, 22°7′N, 81°8′W, Bolira Cochinos, Santa Clara [Prov.], Cuba, 180–190 fth.); holotype MCZ 135245.

bermudezi Clench & Aguayo, *Columbarium* 1938, Mem. Soc. Cubana Hist. Nat., **12:** 383, pl. 28, fig. 7 (*Atlantis* Sta. 2989, 23°10′N, 80°4′W, off Sagua la Grande, Cuba, 360 fth.); holotype MCZ 135007.

bermudezi Clench, *Liguus flammellus* 1934, Occas. Pap. Boston Soc. Nat. Hist., **8:** 122, pl. 6, fig. 2 (Mogote la Gueca Viñales, Pinar del Rio, Cuba); holotype MCZ 80945.

bermudezi Clench & Aguayo, *Mecoliotia* 1936, Nautilus, **49:** 92, pl. 5, fig. 3 (0.5 km S of the mouth of Rio Canimar, Matánzas, Cuba); holotype MCZ 110615.

bermudezi Clench & Aguayo, *Orthaulax* 1939, Mem. Soc. Cubana Hist. Nat., **13**(5): 357, pls. 47, 48 (Paso Real de San Diego, Pinar del Rio Prov., Cuba, in a well at a depth of 10 ft.); holotype MCZ 27936.

bigelowi Clench & Aguayo, *Calliostoma* (*Astele*) 1938, Mem. Soc. Cubana Hist. Nat., **12:** 378, pl. 28, figs. 4, 5 (*Atlantis* Sta. 2963-c, Bahia Cochinos, Cuba, 205 fth.); holotype MCZ 135003.

Bigelowia (genus) Macdonald & Clench, 1934, Occas. Pap. Boston Soc. Nat. Hist., **8:** 145 (type species, *Bigelowia atlanticus,* Macdonald and Clench 1934, original designation).

blainei Clench & Turner, *Epitonium* (*Boreoscala*) 1953, Johnsonia, **2:** 361, pl. 180 (about 45 mi. SW of the light house, Boca Grande, Florida); holotype MCZ 189246.

blakei Clench & Aguayo, *Calliostoma* (*Calliostoma*) 1938, Mem. Soc. Cubana Hist. Nat., **12:** 376, pl. 28, fig. 6 (*Hassler* exped., 41°17′S, off Cape Bermeja, Argentina, 17 fth.); holotype MCZ 89661.

blanesi Clench & Aguayo, *Caracolus sagemon* 1951, Mem. Soc. Cubana Hist. Nat., **20:** 68, pl. 42, figs. 7, 8 (Silla de Gibara, Oriente, Cuba); holotype Museo Poey 17302, paratypes MCZ 76974.

blanesi Clench & Agauyo, *Cerion* 1951, Rev. Soc. Malacól. "Carlos de la Torre," **8:** 70, pl. 11, fig. 1 (Los Cocos, E side of Bahía de Gibara, Cuba); holotype Museo Poey 17266, paratype MCZ 52784.

blanesi Clench & Aguayo, *Emoda* 1953 [in] Aguayo, Mem. Soc. Cubana Hist. Nat., **21:** 301, pl. 35, figs. 1, 2 ("Embarradas," al Norte de Banes, Oriente, Cuba); holotype Museo Poey 17324, paratype MCZ [not received].

bollingi Clench, *Oliva reticularis* 1934, Nautilus, **47:**

142, pl. 7, figs. 3, 4 (off Miami, Florida, crab traps at 200 ft.); holotype MCZ 76656.

bottimeri Clench, *Physa* 1924, Nautilus, **38:** 12, text fig. 4 (Comanche Spring, Fort Stockton, Pecos Co., Texas); holotype UMMZ 31617, paratypes MCZ 53866, 86375.

boultoni 'Bequaert and Clench' Parodiz & Tripp, *Viviparus* (*Bellamya*): 1988, Ann. Carnegie Mus., **57**(5): 130 [nomen nudum].[2]

branchi Clench, *Murex* (*Murex*) 1953, Johnsonia, **2:** 360, pl. 179 (Gulf of Campeche, Yucatan, Mexico); holotype MCZ 201474.

branhamae Clench, *Conus jaspideus* 1953, Johnsonia, **2:** 364, pl. 181, fig. 2 (Green Turtle Cay, Great Abaco, Bahama Islands); holotype AMNH 166926.

brasiliensis Clench, *Conus* 1942, Johnsonia, **1**(6): 24, pl. 12, fig. 2 (*Thayer* exped., Victoria, Brazil); holotype MCZ 146894.

brayi Clench, *Columbarium* 1959, Johnsonia, **3:** 330, pl. 173 (*Atlantis* cruise 240, 11°N, 66°1′W, off Cabo Codera, Venezuela, 150 fth.); holotype MCZ 221601.

brazieri Clench, *Dublonia* 1949, Bull. B. P. Bishop Mus., (196): 8, fig. 2 (Mt. Tolowan, Dublon Island, Truk Islands, Caroline Islands); holotype Bishop Museum 153355, paratypes Bishop Museum 153720, MCZ 140532 from Neborus, Muen Island, Truk Islands.

brooksi Bequaert & Clench, *Achatina* (*Pintoa*) 1934, Rev. Zool. Bot. Afr., **24**(3): 271, pl. 1, figs. 3, 7 (Clauca, Angola); holotype Carnegie Mus., 62.25670 (only specimen).

brooksi Gustafson, Turner, Lutz & Vrijenhoek, *Bathymodiolus* 1998, Malacologia, **40**(1–2): 78, figs. 11–15 (*Alvin* Dive 2211, 26°21.3′N, 94°29.7′W, in the western Gulf of Mexico at a hydrocarbon seep in Alaminos Canyon, 2,222 m); holotype ANSP A1884/18847, paratypes MCZ 316973–6.

bullisi Clench & Turner *Calliostoma* (*Elmerlinia*) 1960, Johnsonia, **4:** 36, pl. 5, fig. 1; pl. 9, fig. 2; pl. 23 (*Oregon* Sta. 2049, 4°2′N, 50°33′W, about 65 mi. ESE of Cabo Orange, Arnapá, Brasil, 38 fth.); holotype USNM 612702.

burryae Clench, *Conus floridanus* 1942, Johnsonia, **1**(6): 29, pl. 14, figs. 3, 4 (off Lower Matecumbe Key, Florida); holotype MCZ 145296.

burryi Clench & Pérez Farfante, *Murex* (*Poirieria*) 1945, Johnsonia, **1**(17): 47, pl. 24, figs. 1–3 (off Fort Walton, Florida, 13–19 fth.); holotype MCZ 164567.

burryi Clench & Turner *Opalia* (*Dentiscala*) 1950, Johnsonia, **2:** 235, pl. 102, figs. 1–3 (4.5 mi. off Carysfort Light, Key Largo, Florida, 92–100 fth.); holotype MCZ 187107.

butleri Clench, *Scaphella junonia* 1953, Johnsonia, **2:** 377, pl. 186, fig. 3 (Bay of Campeche, Yucatan, Mexico); holotype MCZ 193591.

cadenasi Clench & Aguayo, *Tylotia* 1939, Mem. Soc. Cubana Hist. Nat., **13:** 195, pl. 29, fig. 5 (*Atlantis* Sta. 2963, 22°7′N, 81°8′W, Bahía de Cochinos, Cuba, 180 fth.); holotype MCZ 135056.

cahabensis Clench, *Clappia* 1965, Nautilus, **79:** 33, text fig. 2 (Cahaba River, 1 mi. N of Centreville, Bibb Co., Alabama); holotype MCZ 251167.

caicosense Clench, *Cerion* (*Strophiops*) 1937, Proc. N. Engl. Zool. Club, **16:** 23, pl. 1, fig. 4 (Cockburn Town, South Caicos Island, Turks Islands); holotype MCZ 116021.

calciphila Cooke & Clench, *Fijianella* 1943, Occas. Pap. B. P. Bishop Mus., **17**(20): 258, fig. 7 (Yaugasa Levu, Lau Islands, Fiji Islands); holotype Bishop Museum 10107, paratypes MCZ 137107.

caledoniensis Clench & Jacobson, *Emoda* 1971, Bull. Mus. Comp. Zool., **141:** 112, pl. 2, figs. 11, 12, pl. 5 (Mina Caledonia, Mayari, Oriente, Cuba); holotype MCZ 261352.

candefacta Bequaert & Clench, *Archachatina* (*Megachatinops*) *adelinae* 1936, Rev. Zool. Bot. Afr., **29**(1): 87 (Johann Albrechtshöhe, Cameroon); holotype MCZ 79972.

canetae Clench & Aguayo, *Buccinum* 1944, Rev. Soc. Malacól. "Carlos de la Torre," **2**(1): 67–68, text fig. (*Atlantis* Sta. 3003, 23°12′30″N, 82°12′W, off Havana, Cuba, 240–300 fth.); holotype MCZ 145740.

carbonarius Clench, *Liguus flammellus* 1934, Occas. Pap. Boston Soc. Nat. Hist., **8:** 121, pl. 6, fig. 3 (Mogote de Pita, Viñales, Pinar del Rio, Cuba); holotype MCZ 80933.

carcellesi Clench & Aguayo, *Calliostoma* (*Calliostoma*) 1940, Mem. Soc. Cubana Hist. Nat., **14**(1): 80, pl. 14, fig. 4 (*Hassler* voyage, 40°22′S, 60°35′W, off Punta Rubio, Argentina, 30 fth.); holotype MCZ 104719.

caribaea Clench & Aguayo, *Poteria* 1935, Nautilus, **49:** 51, pl. 3, figs. 5, 6 (Spring Mount, St. James, Jamaica); holotype MCZ 109264.

caribaeus Clench, *Liguus fasciatus* 1935, Nautilus, **49:** 68, pl. 3, fig. 3 (Moute Dios, Santa Lucia, N coast of Pinar del Rio, Cuba); holotype MCZ 109050.

caribbaea Clench & Aguayo, *Oocarys sulcata* 1939, Mem. Soc. Cubana Hist. Nat., **13:** 192, pl. 29, fig. 3 (*Atlantis* Sta. 2953, 21°47′30″N, 84°30′30″W, Bahía de Corrientes, Pidelkio, Cuba, 615 fth.); holotype MCZ 135072.

caribbaea Clench, *Urocoptis* (*Urocoptola*) 1966, Breviora, (245): 9, pl. 1, fig. 3 (1 mi. E of Pointe à Raquette, South Central Gonave Island, Haiti); holotype MCZ 260873.

caribbaeum Clench & Turner, *Cymatium* (*Ranularia*) 1957, Johnsonia, **3:** 204, pl. 111, figs. 3, 4, pl. 113, fig. 3, p. 117, figs. 1, 2 (new name for *Triton cynocephalum* 'Lam.' Kiener 1842, non *T. cynocephalum* Lamarck 1816).

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[2] PARODIZ, J. J., AND J. J. TRIPP. 1988. Types of Mollusca in the collection of the Carnegie Museum of Natural History Part I. Bivalvia and Gastropoda (Prosobranchia and Opisthobranchia) Annals of the Carnegie Museum, **57**(5): 111–154.

caribbea Clench & Turner, *Bankia* (*Bankopsis*) 1946, Johnsonia, **2**(19): 16, pl. 10, figs. 1–4 (Fort Pickens, Pensacola, Florida); holotype MCZ 121065.

carinata Clench & Aguayo, *Jeanneretia parraina* 1951, Rev. Soc. Malacól. "Carlos de la Torre," **7**(3): 86, pl. 14, figs. 8, 9 (Mogote de la Resbalosa, Laguna de Piedras, Viñales, Cuba); holotype Museo Poey 16001, paratypes MCZ [not received].

carnicolor Clench & Pérez Farfante, *Murex* (*Murexsul*) 1945, Johnsonia, **1**(17): 48, pl. 25, figs. 1–4 (*Blake* Sta. 273, off Barbados, 103 fth.); holotype MCZ 7305.

carolae Clench, *Ficus* 1945, Johnsonia, **18:** 3, pl. 2 (5.5 mi. SE of The Elbow, Key Largo, Florida, 92–100 fth.); holotype MCZ 157501.

carribaeus Clench, *Conus* 1942, Johnsonia, **6:** 23, pl. 11, figs. 4, 5 (off Palm Beach, Florida); holotype MCZ 138333.

castilloi Clench & Jaume, *Helicina* (*Helicina*) 1946, Rev. Soc. Malacól. "Carlos de la Torre," **4:** 7–8, text figs. 1–3 (Rancho Arriba, San José de Ocoa, Prov. de Azua, Républica Dominicana); holotype MCZ 155149.

cayemitensis Clench, *Urocoptis* (*Urocoptola*) 1966, Breviora, (245): 7, pl. 1, fig. 4 (NE Grande Cayemite, 6.5 mi. NE of Corail, Dépt. du Sud, Haiti); holotype MCZ 254666.

cecilae Wetherbee & Clench, *Macroceramus* 1984, Caribb. J. Sci., **20**(1–2): 11, fig. 1, pl. 1, pt. B, center (top of Mt. Isabel de Torres, Puerto Plata Prov., República Dominicana, 2,500 ft.); holotype MCZ 75450.

ceiba Clench, *Cerion* 1948, Rev. Soc. Malacól. "Carlos de la Torre," **6**(2): 49, figs. 1–3 (N side of Boca del Rio Jibacoa, Santa Cruz del Norte, Havana Prov., Cuba); holotype MCZ 157307.

Celetaia (genus) Clench 1966, Nautilus, **79:** 137 (type species, *Vivipara persculpta* P. & F. Sarasin 1898, original designation).

cerosa Clench & Aguayo, *Hemitrochus* 1937, Mem. Soc. Cubana Hist. Nat., **11**(2): 76, pl. 7, fig. 5 (La Visite, La Selle Range, Haiti); holotype MCZ 110620.

cervus Clench, *Liguus flammellus* 1934, Occas. Pap. Boston Soc. Nat. Hist., **8:** 120, pl. 6, fig. 4 (Mogote de Vigil, Viñales, Pinar del Rio, Cuba); holotype MCZ 80935.

Chaceia (genus) Turner, 1955, Johnsonia, **3**(34): 66 (type species, *Pholas ovoidea* Gould, 1851, original designation).

championi Clench & Turner, *Epitonium* (*Asperiscala*) 1952, Johnsonia, **2:** 318, pl. 153 (Lewis Bay, Hyannis, Cape Cod, Massachusetts); holotype MCZ 182900.

chapini Bequaert & Clench, *Achatina rugosa* 1934, Am. Mus. Novit., (705): 4, text fig. 2 (Lukolela, Belgian Congo); holotype AMNHA 6438, paratype MCZ 93211.

chapini Bequaert & Clench, *Maizania* (*Maizaniella*) *lukolelensis* 1936, Rev. Zool. Bot. Afr., **29**(1): 101 (New Beni [Bungula], Belgian Congo); holotype MCZ 102375.

chengi Turner & Santhakumaran, *Lignopholas* 1989, Ophelia, **30**(3): 180, figs. 17–19 (Semariang, Sarawak about 1.6 km up Semariang River, a tributary of the Santubong River about 8.7 km from the mouth); holotype MCZ 207208, paratypes MCZ 297209.

childressi Gustafson, Turner, Lutz & Vrijenhoek, "*Bathymodiolus*" 1998, Malacologia, **40**(1–2): 84, figs. 11–13, 16–20 (*Johnson Sea-Link-1*, 27°46.9′N, 91°30.4′W, about 210 km SSW of Grand Isle, Louisiana, 546 m); holotype ANSP A18848, paratype MCZ 316978.

chondrocycloides Bequaert & Clench, *Maizania* (*Maizaniella*) 1936, Rev. Zool. Bot. Afr., **29**(1): 101 (village of Malela, 5°40′S, 23°45′E, Belgian Congo); holotype MCZ 109548.

christophei Clench, *Cerion* 1937, Proc. N. Engl. Zool. Club, **16:** 24, pl. 1, fig. 2 (northeast Point [Christophies Palace], Great Inagua Island, Bahamas); holotype MCZ 116006.

ciboney Clench & Pérez Farfante, *Murex* (*Murex*) 1945, Johnsonia, **1**(17): 20, pl. 10, figs. 1–3 (*Atlantis* Sta. 3482, 23°9′N, 81°27′30″W off Matánzas, Cuba, 190 fth.); holotype MCZ 147315.

cieba Clench & Turner, *Bankia* (*Plumielella*) 1946, Johnsonia, **2**(19): 25, pl. 16, figs. 1–4 (Balboa, Canal Zone, Panama); holotype MCZ 168097.

cisnerosi Clench & Aguayo, *Cerion* 1951, Rev. Soc. Malacól. "Carlos de la Torre," **8:** 72, pl. 11, figs. 3, 4 (Playa Morrillo, 11 km W of Bahía Honda, Pinar del Rio, Cuba); holotype Museo Poey 12667, paratypes MCZ 187317.

clappii Turner, *Lignopholas* 1955, Johnsonia, **3**(34): 99, pl. 60 (Bluefields, Nicaragua); holotype MCZ 200046.

clementis Clench & Aguayo, *Emoda* 1950, Rev. Soc. Malacól. "Carlos de la Torre," **7:** 62, pl. 12, figs. 4, 5 (Cayo del Rey, Mayari, Oriente, Cuba); holotype Museo Poey 12923, paratypes MCZ 185799.

clenchi Turner, *Hemitrochus* 1958, Occas. Pap. Mollusks, **2**(22): 161–164, pl. 23, figs. 3, 4; pl. 24, figs. 7, 8; pl. 25; pl. 30, fig. 2 (Maricao Forest, Puerto Rico); holotype MCZ 216146.

clenchi Turner & Culliney, *Xylophaga* 1971, American Malacological Union Annual Report for 1970, p. 66 (24°54′N, 77°49′W), Tongue of the Ocean, about 4 mi. off NE tip of Andros Island, Bahamas); Turner, 2002, Bull. Mus. Comp. Zool., **157**(4): 239 pls. 5–8; holotype MCZ 316743, paratypes MCZ 316744, 316745.

cliffordi Clench, *Cerion* (*Strophiops*) *martensi* 1933, Proc. N. Engl. Zool. Club, **13:** 91, pl. 1, fig. 10 (Landrail Pt., Crooked Island, Bahamas); holotype MCZ 101153.

coeruleus Clench & Archer, *Amphidromus* 1932, Occas. Pap. Boston Soc. Nat. Hist., **8:** 41, pl. 4, figs. E, F (0.5 mi. above Fort at Long Loba, Tinja River, Sarawak, Borneo); holotype MCZ 44991, paratype MCZ 247891.

congolensis Bequaert & Clench, *Septariellina* 1936, Mem. Mus. R. Hist. Nat. Belg., 2nd ser., (3): 163, fig. 1 (Ango-Ango, 4 km S of Matadi, Congo River, Belgian Congo); holotype MCZ 59807.

cookei Clench, *Lyropupa* 1952, B. P. Bishop Museum, Special Publication 42, p. 32 (new name for *Lyropupa anceyana* Cooke & Pilsbry 1920, non *Lyropupa aceyana* Pilsbry & Cooke 1920).

cookei Clench, *Ostodes* 1949, Bull. B. P. Bishop Museum 196, p. 10, fig. 3a (Tiavi, Upolu Island, Samoan Islands); holotype Bishop Museum 9711, paratype MCZ 140504.

cookei Clench, *Placostylus* (*Eumeocostylus*) *oleryi* 1941, Am. Mus. Novit., (1129): 16 (Waiai, San Christoval Island, Solomon Islands); holotype MCZ 65996.

cookei Cl & Turner, *Taheitia arcasiana* 1948, Occas. Pap. Mollusks, **1**(13): 186, pl. 23, fig. 3 (Vuni Vatu, central Viti Levu, Fiji Islands); holotype MCZ 181049.

cookei Clench, *Thaanumella* (*Jokajia*) 1946, Occas. Pap. B. P. Bishop Mus., **18**(13): 204, text fig. 4 (base of Peipalop Peak, Ponape, Caroline Islands); holotype Bishop Museum 189004, paratypes MCZ 140590.

cookei Clench, *Tylotoechus* 1949, Bull. B. P. Bishop Mus., **196:** 44, fig. 25 (Auki, Malaita Island, Solomon Islands); holotype MCZ 141013, paratypes Bishop Museum 188849.

cornucopia Cooke & Clench, *Fijianella* 1943, Occas. Pap. B. P. Bishop Mus., **17**(20): 260, fig. 86 (Navutu Iloma, Lau Islands, Fiji Islands); holotype Bishop Museum 10109, paratypes MCZ 137108.

coultasi Clench, *Dendrotrochus* 1957, Am. Mus. Novit., (1863): 4, fig. 6 (Masahet Island, Lihir Group, Bismarck Archipelago); holotype AMNH 73487, paratypes MCZ 188142.

coultasi Clench *Pseudocyclotus* 1957, Am. Mus. Novit., (1863): 1, figs. 1, 2 (Tavi Village, Manus Island, Admiralty Islands); holotype AMNH 73485, paratypes MCZ 188141.

coultasi Clench, *Quirosella* 1958, Natural History of Rennell Island, British Solomon Islands, Copenhagen, Denmark, **2:** 175, pl. 18, figs. 1, 2, text fig. 2 (Rennell Island, Solomon Islands); holotype AMNH 59011, paratypes MCZ 93018.

coutini Clench & Aguayo *Caracolus sagemon* 1951, Mem. Soc. Cubana Hist. Nat., **20:** 66, pl. 42, figs. 1–4 (Nibujón, 4 km NW of Baracoa, Oriente, Cuba); holotype Museo Poey 17300, paratypes MCZ 181892.

cramptoni Clench, *Partula* 1941, Am. Mus. Novit., (1129): 20, fig. 13 (Rennell Island, Solomon Islands); holotype AMNH 79014, paratypes MCZ 93201, 100381.

Cristovala (subgenus) Clench, 1958, Natural History of Rennell Island, British Solomon Islands, Copenhagen, Denmark, **2:** 188 (type species, *Crystallopsis tricolor* (Pfeiffer, 1849), original designation).

crystallina Clench, *Crystallopsis* (*Crystallopsis*) 1958, Natural History of Rennell Island, British Solomon Islands, Copenhagen, Denmark, **2:** 182, pl. 16, fig. 5 (Ulawa Island, Solomon Islands); holotype AMNH 66484, paratypes 66441, paratypes MCZ 92945.

cuba Clench, *Scaphella* (*Aurinia*) 1946, Johnsonia, **2**(22): 58, pl. 31, fig. 2 (*Atlantis* Sta. 2988, 23°15′N, 79°57′W, off Sagua la Grande, Las Villas, Cuba, 380 fth.); holotype MCZ 135229.

cubana Clench & Aguayo, *Cochlespira* (*Ancistrosyrinx*) *radiata* 1940, Mem. Soc. Cubana Hist. Nat., **14**(1): 94, pl. 15, fig. 1 (*Atlantis* Sta. 3332, 22°9′30″N, 81°11′W, Bahía Cochinos, Santa Clara Prov., Cuba, 175–225 fth.); holotype MCZ 135194.

cubana Clench & Aguayo, *Gaza superba* 1940, Mem. Soc. Cubana Hist. Nat., **14**(1): 81, pl. 15, fig. 3 (*Atlantis* Sta. 3448, 23°21′N, 79°56′W, off Sagua la Grande, Santa Clara Prov., Cuba, 380 fth.); holotype MCZ 135151.

cubanum Clench & Aguayo, *Calliostoma* (*Calliostoma*) 1940, Mem. Soc. Cubana Hist. Nat., **14:** 78, pl. 16, fig. 4 (*Atlantis* Sta. 3474, 23°18′N, 80°46′W, off Cardenas, Matangas Prov., Cuba, 490 fth.); holotype MCZ 135163.

cubensis Clench, *Liguus flammellus* 1934, Occas. Pap. Boston Soc. Nat. Hist., **8:** 123, pl. 6, fig. 1 (Mogote la Gueca, Viñales, Pinar del Rio, Cuba); holotype MCZ 80951.

Culmenella (subgenus) Clench, 1927, Nautilus, **40:** 121, fig. 1 (type species, *Bulinus* [*Culmenella*] *hirasei* Clench 1927, monotypy).

Cymatriton (subgenus) Clench & Turner, 1957, Johnsonia, **3:** 210 (type species [*Cymatium*] *nicobaricum* Röding 1789, original designation).

darlingtoni Clench, *Archegocrptis* 1935, Proc. Boston Soc. Nat. Hist., **41**(1): 6, pl. 1, figs. C, G (Tardieu, Mt. La Hotte, Haiti, 3,000 ft.); holotype MCZ 108592.

darlingtoni Clench, *Brachypodella* (*Brachypodella*) 1935, Proc. Boston Soc. Nat. Hist., **41:** 10, pl. 2, fig. H (Miragoane, Haiti); holotype MCZ 108588.

darlingtoni Clench, *Hemitrochus* 1964, Rev. Mus. Argent. Cienc. Nat. "Bernardino Rivadavia," **8:** 223, pl. 1, fig. 4 (Loma Pelona, near Loma Rucilla [Pico Trujillo] Prov. de Santiago, Républica Dominica, 9,000–10,000 ft.); holotype MCZ 187934.

darlingtoni Bequaert & Clench, *Mcleania* 1939, Mem. Soc. Cubana Hist. Nat., **13:** 283, pl. 36, figs. 4–6 (Maricao Forest, western Puerto Rico, 2,500 ft.); holotype MCZ 90736.

darlingtoni Clench & Aguayo, *Parachondria* (*Parachondria*) 1937, Mem. Soc. Cubana Hist. Nat., **11**(2): 66, pl. 7, fig. 4 (Poste Terre Rouge, Haiti, 2,000 ft.); holotype MCZ 108576.

darlingtoni Clench & Archer, *Thersites* 1938, J. Conch., **21:** 20, pl. 1, fig. 2 (MacPherson Range, Queensland Nat. Park, 60 mi. S of Brisbane, Queensland); holotype MCZ 99054, paratype Queensland Museum, South Brisbane, Queensland (UMMO) 1766.

deckerti Clench, *Liguus fasciatus* 1935, Nautilus, **48:**

122, pl. 7, fig. 4 (Hammock 55, E end of Long Pine Key, South Central Everglades, Florida); holotype MCZ 81549.

degeneri Clench, *Cerion* 1948, Rev. Soc. Malacól. "Carlos de la Torre," **6**(2): 50, figs. 4–6 (Fleeming Point, New Providence Island, Bahamas); holotype MCZ 175065.

degneri Bequaert & Clench, *Archachatina* (*Magachatina*) 1936, Rev. Zool. Bot. Afr., **29**(1): 78, pl. 1, fig. 1 (Duma, Ubangi Dist., Belgian Congo); holotype Zoological Museum, Hamburg (ZMH) 2893 (only specimen).

degneri Bequaert & Clench, *Ptychotrema* (*Ptychotrema*) 1936, Nautilus, **49**(3): 96, pl. 6, figs. 3, 4 (Africa); holotype MCZ 10939.

delli Clench, *Palaina* (*Palaina*) 1965, Breviora, (224): 6, pl. 2, fig. 5 (W side of the Lunga River, 0.5 mi. above the Seventh Day Adventist Mission Station on Guadalcanal Island, Solomon Islands); holotype MCZ 258017, paratypes MCZ 258018.

demesana Clench & Archer, *Helicostyla cincinniformis* 1931, Occas. Pap. Boston Soc. Nat. Hist., **5:** 336, pl. 17, fig. 5 (Lubang Island, Philippines); holotype MCZ 79171, paratypes MCZ 47216.

depalmai Turner, *Xylophaga* 2002, Bull. Mus. Comp. Zool. **157**(4): 253, pls. 23, 24 (26°4′N, 80°4′W, about 3.2 mi. off Fort Lauderdale, Florida, 152.4 m); holotype MCZ 316735.

depressa Clench & Aguayo *Jeanneretia parraiana* 1951, Rev. Soc. Malacól. "Carlos de la Torre," **7:** 85, pl. 13, figs. 10–12 (Hoyo del Guamá, Viñales, Pina del Rio, Cuba); holotype Museo Poey 17207, paratypes 181710, 181714.

destructa Clench & Turner, *Bankia* (*Neobankia*) 1946, Johnsonia, **2**(19): 20, pl. 13, figs. 1–4 (La Cieba, Honduras); holotype MCZ 123303.

dewittei Bequaert & Clench, *Achatura* (*Pintoa*) 1934, Rev. Zool. Bot. Afr., **24:** 270, pl. 1, fig. 428 (Nyonga, region of Lahe Upemba, Katanga Dist., Belgian Congo); holotype MRAC 7592, paratypes MRAC 7593–7604, 7605–7625, MCZ 81986.

dewulfi Bequaert & Clench, *Pila* 1933, Rev. Zool. Bot. Afr., **23:** 71, pl. 5 (Inkisi River near Kisantu, Belgian Congo); holotype MCZ 92101.

diagonalis Clench, *Urocoptis* (*Gongylostoma*) 1966, Breviora, (245): 6, pl. 2, fig. 4 (Mina Carlota, Siervade San Juan, 8 mi. S of Cumanayagua, Las Villas, Cuba); holotype MCZ 59292.

dickinsoni Clench & Turner, *Goniobasis* 1956, Bull. Fla. State Mus., **1**(3): 141, pl. 2, fig. 10 (Holmes Creek, 1 mi. W of Graceville, Florida); holotype MCZ 191771.

disforme Clench & Aguayo, *Cerion* 1946, Rev. Soc. Malacól. "Carlos de la Torre," **4:** 85, text figs. 1–6 (Cercanías de Punta Manolito, Península del Ramón, Antilla, Oriente, Cuba); holotype MCZ 166621.

dolphin Clench & Cooke, *Succinea wallisi* 1945, Occas. Pap. B. P. Bishop Museum, **18**(8): 134, fig. 2 (Tautira Valley, Taiarupu Peninsula, Tahiti, Society Islands); holotype Bishop Museum, 9715, paratype MCZ 146392.

dominicana Clench, *Coryda* 1964, Rev. Mus. Argent. Cienc. Nat. "Bernardino Rivadavia," **8:** 224, pl. 1, fig. 2 (Yuma, Prov. de El. Seibo, República Dominicana); holotype MCZ 188239.

domincanum Clench & Aguayo, *Cerion marielinum* 1951, Rev. Soc. Malacól. "Carlos de la Torre," **8:** 69, pl. 10, figs. 1–3 (E side of Boca del Rio Dominica about 10 mi. W of Mariel, Cuba); holotype MCZ 181904, paratype Museo Poey 12670.

Dublonia (genus) C1., 1949, Bull. B. P. Bishop Mus., (196): 7 (type species, *Dublonia brazieri* Clench, 1949, original designation).

Echininus Clench & Abbott, 1942, Johnsonia, **1**(4): 3 (new name for *Nina* Gray 1850, non Horsfield 1829).

edentula Clench, *Coryda* 1964, Rev. Mus. Argent. Cienc. Nat. "Bernardino Rivadavia," **8:** 226, pl. 2, fig. 3 (Bahía de San Lorenzo, Bahía de Samaná, Prov. de Samaná, Républica Dominicana); holotype MCZ 188243.

egregiella Bequaert & Clench, *Archachatina marginata* (*Megachatina*) 1936, Rev. Zool. Bot. Afr., **29:** 83, pl. 1, fig. 3 (Kiribi, Cameroon); holotype MCZ 73135.

ekmani Clench, *Urocoptis* (*Urocoptola*) 1966, Breviora, (245): 8, pl. 1, fig. 5 (La Source, NW Gonave Island, Haiti); holotype MCZ 260871.

elegans Clench & Aguayo, *Physa* (*Haitia*) 1932, Proc. N. Engl. Zool. Club, **13:** 37 (Lake Miragoane, 2 mi. SE of Miragoane, Haiti); holotype MCZ 83736, paratypes MCZ 837382.

Elmerlinia (subgenus) Clench & Turner, 1960, Johnsonia, **4:** 29 (type species, *Callistoma jujubinum* Gmelin 1791, original designation).

eolis Clench & Turner, *Opalia* (*Nodiscala*) 1950, Johnsonia, **2:** 241, pl. 105, figs. 1–3, pl. 107, fig. 4 (off Looe Key, Lower Florida Keys, 70–90 fth.); holotype MCZ 187110.

eriksoni Clench, *Cerion* (*Maynardia*) 1959, Bull. Mus. Comp. Zool., **121**(2): 48, pl. 1, fig. 1 (Southwest Point, Little Inagua, Bahama Islands); holotype MCZ 189121.

escambia Clench & Turner, *Fusconaia* 1956, Bull. Florida State Museum, **1**(3): 152, pl. 7, figs. 3, 4 (Escambia River, 3 mi. SE of Century, Escambia Co., Florida); holotype MCZ 191470.

Euaethiops genus Clench & Archer, 1930, Occas. Pap. Boston Soc. Nat. Hist., **5:** 295 (type species *Euaethiops loveridgei* Clench & Archer 1930, original designation).

euglypta Clench & Aguayo, *Alcadia* 1950, Rev. Soc. Malacól. "Carlos de la Torre," **7:** 64, pl. 12, figs. 6–8 (Cerro Cariblanco, Holguín, Oriente, Cuba); holotype Museo Poey 12911, paratypes MCZ 185797.

evelynae Clench & Aguayo, *Terebra* 1939, Mem. Soc. Cubana Hist. Nat., **13:** 196, pl. 29, fig. 1 (*Atlantis* Sta. 2981, 22°48′N, 78°48′W, off northern Santa

Clara Prov., Cuba, 225 fth.); holotype MCZ 135077.

evelynae Clench, *Urocoptis* (*Autocoptis*) 1935, Proc. Boston Soc. Nat. Hist., **41:** 4, pl. 1, figs. D–H (north foothills of Mt. La Hotte, Haiti, 3,000 ft.); holotype MCZ 108597.

exhuberans Clench & Aguayo, *Caracolus sagemon* 1951, Mem. Soc. Cubana Hist. Nat., **20:** 67, pl. 41, figs. 7, 8 (Cercenías de Baracoa, Oriente, Cuba); holotype Museo Poey 17301, paratypes MCZ 87543 labeled, Boca de Jauco, Gan Tierra, Baracoa, Oriente, Cuba).

exquisita Clench, *Urocoptis* (*Gongylostoma*) 1966, Breviora, (245): 5, pl. 2, fig. 2 (0.5 mi. E of Guabairo, Soledad, Cienfuegos, Cuba); holotype MCZ 59286.

eyerdami Clench & Banks, *Anguispira kochi* 1939, Mem. Soc. Cubana Hist. Nat., **13:** 285, pl. 36, fig. 3 (46°30′N, 120°38′W, slope near mountaintop, Horse Haven Hills, Yakima Indian Reservation, Washington. [This locality is] 75 mi. from Satus Creek and 10 mi. S of Alfalfa, Washington); holotype MCZ 100491.

eyerdami Clench & Aguayo, *Helisoma* 1932, Proc. N. Engl. Zool. Club, **13:** 38 (Lake Miragoane, 2 mi. SE of Miragoane, Haiti); holotype MCZ 83887, paratypes MCZ 83883.

eyerdami Clench, *Nesopoma* 1958, Natural History of Rennell Island, British Solomon Islands, Copenhagen, Denmark, **2:** 169, pl. 17, fig. 4 (Su'u, Malaita, Solomon Islands); holotype AMNH 73885, paratypes MCZ 188086.

fairchildi Clench, *Asolene* (*Surinamia*) 1933, Nautilus, **47:** 71, pl. 7, figs. 1, 2 (on rocks in the Cataract of the Surinam River below Kedjo, 100 mi. upriver from Paramaribo, Dutch Guiana); holotype MCZ 80515.

fairchildi Clench, *Cerion* (*Strophiops*) 1933, Proc. N. Engl. Zool. Club, **13:** 97, pl. 1, fig. 6 (Conception Island, Bahamas); holotype MCZ 80502, paratypes MCZ 80503.

fairchildi Clench, *Liguus blainianus* 1934, Occas. Pap. Boston Soc. Nat. Hist., **8:** 117, pl. 7, fig. 4 (road between Havana and Santiago de las Vegas, Havana Prov., Cuba); holotype MCZ 91907.

fairchildi Bequaert & Clench, *Solaropsis gibboni* 1938, Nautilus, **51:** 115, pl. 9, figs. 6, 7 (Anapolis, Goyas, Brasil); holotype MCZ 65208; paratypes MCZ 65209.

farnumi Clench, *Liguus crenatus* 1929, Nautilus, **43:** 19 (Hammock #7, Pinecrest Region, the Everglades, Florida); holotype MCZ 84586.

fasciata Clench, *Sulcobasis* (*Goldielix*) 1957, Am. Mus. Novit., (1863): 6, fig. 4 (Lorengau, Manus Island, Admiralty Islands); holotype MCZ 190157.

feriai Clench & Aguayo, *Cerion vulneratum* 1953, Torreia, (18): 3, text fig. 6 (Cayo Largo o de los Muertos, Bahía o Puerto Naranjo, Oriente, Cuba); holotype Museo Poey 17247, paratype MCZ 83152.

feriai Clench, *Liguus fasciatus* 1934, Occas. Pap. Boston Soc. Nat. Hist., **8:** 108, pl. 7, fig. 6 (La Sierra, Holguín, Oriente, Cuba); holotype MCZ 72559.

fernandina Clench, *Cerion* 1937, Nautilus, **51:** 21, pl. 3, fig. 5 (Millers, 8 mi. SE of Simms, Long Island, Bahamas); holotype MCZ 65131.

Fijianella (genus) Cooke & Clench, 1943, Occas. Pap. B. P. Bishop Mus., **17**(20): 257 (type species *Fijianella calciphila* Clench & Cooke 1943, original designation).

Fijiopoma (genus) Clench, 1949, Bull. B. P. Bishop Mus., (196): 23 (type species *Ostodes liberatus* Garrett 1887, original designation).

finlayi Clench, *Murex* (*Murex*) 1955, Breviora, (44): 1–3, text figs. 1–3 (shell trap, Matánzas Bay, Cuba, 100 fth.); holotype MCZ 189939.

fisheri Gustafson, Turner, Lutz & Vrijenhoek, *Tamu* 1998, Malacologia, **40**(1–2): 91, figs. 11–13, 21–23 (*Johnson Sea-Link-1* Dive 3108, 27°46.91′N, 91°30.36′W, Bush Hill hydrocarbon seep, 210 km SSW of Grand Isle, Louisiana, 548 m); holotype ANSP A18849, paratype MCZ 316979.

fitchi Turner, *Penitella* 1955, Johnsonia, **3**(34): 66, pls. 40–42 (Bahía San Bartolomé, Baja California, Mexico); holotype MCZ 189413.

flammellus Clench, *Liguus flammellus* 1934, Occas. Pap. Boston Soc. Nat. Hist., **8:** 119, pl. 6, fig. 7 (Mogote de Roja, Viñales, Pinar de Rio, Cuba); holotype MCZ 80924.

flavipellis Clench & Archer, *Helicostylus* (*Chrysallis*) *mindoroensis* 1933, Pap. Mich. Acad. Sci. Arts Lett., **17:** 548, pl. 58, fig. 5 (Calawagan, Palúan, Mindoro, Philippines); holotype MCZ 81358, paratype 81357.

florida Clench & Aguayo, *Aurinia dohrni* 1940, Mem. Soc. Cubana Hist. Nat., **14**(1): 88, pl. 16, fig. 1, text fig. 1 (new name for *Voluta dubia* Dohrn 1879, non Broderip 1828).

floridanus Clench, *Liguus crenatus* 1929, Nautilus, **43:** 20 (Hammock #8, Pinecrest Region, Central Everglades, Florida); holotype MCZ 84559.

Forbesopomus (genus) Bequaert & Clench 1937, Proc. N. Engl. Zool. Club, **16:** 53, pl. 11 (type species *Forbesopomus atalanta* Bequaert & Clench 1937, original designation).

Forcartia (genus) Clench & Turner 1963, J. Malacol. Soc. Aust., (6): 19 (type species *Papuina buehleri* Rensch 1933, original designation).

fosteri Clench & Turner, *Bankia* (*Plumuletta*) 1946, Johnsonia, **2**(19): 24, pl. 15, figs. 1–4 (Santa Marta, Colombia); holotype MCZ 122536.

fosteri Clench & Aguayo, *Conus* 1942, Johnsonia, **1**(6): 34, pl. 12, fig. 5 (*Atlantis* Sta. 3434, 23°10′N, 79°35′W, off Sagua la Grande, Santa Clara Prov., Cuba); holotype MCZ 146003.

fosteri Clench, *Plagioptycha* 1940, Mem. Soc. Cubana Hist. Nat., **14**(1): 16, pl. 3, fig. 4 (Bret's Hill, Long Island, Bahama Islands); holotype MCZ 113367.

foxi Clench, *Placostylus* (*Eumecostylus*) 1950, Torreia, (15): 1–4, text fig. (9°13′S, 161°27′E, Heuru,

San Cristobal, Solomon Islands); holotype MCZ 187121

Foxidonta (genus) Cl., 1950, Rev. Soc. Malacól. "Carlos de la Torre," **7:** 59 (type species *Foxidonta stevensoni* Clench 1930, monotypy).

freirei Clench & Aguayo, *Emoda* (*Glyptemoda*) 1950, Rev. Soc. Malacól. "Carlos de la Torre," **7:** 61, pl. 12, figs. 1–3 (La Manuela, antes de llegar a la Furnia de la Mina los Negros, Baire, Oreinte, Cuba); holotype Museo Poey 12918, paratype MCZ 185798.

frisbeyae Clench & Pulley, *Conus* 1952, Tex. J. Sci. pp. 59–61, pl. A, fig. 1 (Campeche Bank, Yucatan, Mexico, about 23 fth.); holotype MCZ 187708.

furva Clench & Archer, *Heliostyla* (*Chrysallis*) *mindoroensis* 1933, Pap. Mich. Acad. Sci. Arts Lett., **17:** 546, pl. 58, fig. 3 (Binuangan, Palúan, Mindoro, Philippines); holotype MCZ 81356.

fusiformis Clench & Aguayo, *Metula* 1941, Mem. Soc. Cubana Hist. Nat., **15**(2): 179, pl. 14, fig. 1 (*Atlantis* Sta. 3344, 21°38′N, 80°12′W, off Cienfuegos, Cuba, 1,440 fth.); holotype MCZ 135290.

gaigei Bequaert & Clench, *Choanopoma* 1931, Occas. Pap. Boston Soc. Nat. Hist., **5:** 425 (Chichen Itza, Yucatan); holotype UMMZ 49190, paratypes MCZ 79390 and 79783.

galathea Clench, *Nesopoma* 1930, Natural History of Rennell Island, British Solomon Islands, Copenhagen, Denmark, **2:** 169, pl. 17, fig. 2 (Su'u, Malaita, Solomon Islands); holotype AMNH 73884, paratypes MCZ 188085.

gallegoi Clench, *Placostylus* (*Proaspastus*) 1941, Am. Mus. Novit., (1129): 15, fig. 6 (Mts. of San Christoval Island, Solomon Islands); holotype AMNH 79003, paratype MCZ 92901.

garciana Clench & Aguayo *Cepolis* (*Hemitrochus*) 1953 [in] Aguayo, Mem. Soc. Cubana Hist. Nat., **21:** 308, pl. 35, figs. 8–10 (Caletones, Gibara, Oriente, Cuba); holotype Museo Poey 17303, paratypes MCZ (not received).

garretti Clench *Ostodes* 1949, Bull. B. P. Bishop Mus., (196): 18, fig. 7c (Siavao-Auola, Savaii Island, Samoan Islands); holotype Bishop Museum 108334, paratypes MCZ 140524.

Gasseisia (genus) Clench, 1949, Bull. B. P. Bishop Mus., (196): 5 (type species *Cyclostoma artense* Montrouzier 1859, original designation).

geophilus Clench & Aguayo, *Cerion* 1949, Torreia (Univ. Havana), (14): 5, pl. 1, figs. 7–12 (Punta de Piedra, Banes, Cuba); holotype MCZ 184865, paratypes Museo Poey 7028.

georgiana Clench, *Rehderia* 1946, Johnsonia, **2:** 47, pl. 27, fig. 3 (*Pelican* Sta. 179-5, 31°29.5′N, 79°41.5′W, off Darien, Georgia, 45 fth.); holotype USNM 543509, paratype MCZ 179163.

gerda Turner, *Xylophaga* 2002, Bull. Mus. Comp. Zool. **157**(4): 237, pls. 2, 3 (*Gerda* Sta. 499, 26°37′N, 78°56′W, about 3 mi. off Southwest Point, Great Bahama Island, Bahama Islands, 155 fth.); holotype MCZ 328378, paratypes MCZ 316741, 316742.

gizoensis Clench, *Placostylus* (*Placostylus*) 1941, Am. Mus. Novit., (1129): 5, fig. 10 (Gizo Island, New Georgia Group, Solomon Islands); holotype Bishop Museum 106216, paratype MCZ 106357.

Glyptemoda (section) Clench & Aguayo, 1950, Rev. Soc. Malacól. "Carlos de la Torre," **7:** 61 (type species, *Helicina torrei* Henderson 1909, original designation).

goodrichi Clench, *Liguus faciatus* 1934, Occas. Pap. Boston Soc. Nat. Hist., **8:** 111, pl. 7, fig. 7 (0.75 mi. below Castillo de la Jagua, entrance of Cienfuegos Harbor, Santa Clara, Cuba); holotype MCZ 59533.

goodrichi Clench, *Physa* 1926, Occas. Pap. Mus. Zool., Univ. Mich., (168): 1, pl. 1, figs. 1, 2 (South Fork, Powell River, Big Stone Gap, Virginia); holotype UMMZ 29520, paratypes MCZ 51118.

Goodrichia (genus) Clench, 1929, Bull. Mus. Comp. Zool., **69:** 117 (type species, *Goodrichia trochiformis* Clench 1929, original designation).

gouldi Clench, *Physa* 1935, Nautilus, **49:** 30; ibid, **48**, pl. 7, fig. 5 (Mouse River, 6 mi. N of Towner, McHenry Co., North Dakota); holotype MCZ 103282, paratypes MCZ 103283.

greenwayae Clench, *Oliva reticularis* 1937, Proc. N. Engl. Zool. Club, **16:** 21, pl. 1, fig. 3 (Smith Point, Grand Bahama Island, Bahamas); holotype MCZ 115445.

greenwayi Clench, *Cerion* (*Strophiops*) 1934, Proc. Boston Soc. Nat. Hist., **40**(2): 206, fig. H (Black Booby Cay, West Booby, Atwoods on Samaná Group, Bahama Islands); holotype MCZ 103001.

greenwayi Clench, *Drymaeus bahamensis* 1933, Proc. N. Engl. Zool. Club, **13:** 88, pl. 1, fig. 11 (Landrail Pt., Crooked Island, Bahamas); holotype MCZ 101187.

greenwayi Clench, *Eutrochatella* 1933, Proc. N. Engl. Zool. Club, **13:** 81, pl. 1, fig. 16 (Eleuthera Island, Bahamas); holotype MCZ 90181.

greenwayi Clench, *Microceramus* (*Spiroceramus*) 1938, Mem. Soc. Cubana Hist. Nat., **12:** 329, pl. 25, fig. 1 (Foxtown, Little Abaco Island, Bahama Islands); holotype MCZ 116688.

Guladentia (subgenus) Clench & Aguayo, 1951, Rev. Soc. Malacól. "Carlos de la Torre," **7:** 87 (type species, *Helix subtussulcata* Pfeiffer 1863, original designation).

gundlachi Clench & Aguayo, *Jeanneretia* (*Guladentia*) 1951, Rev. Soc. Malacól. "Carlos de la Torre," **7:** 89, pl. 14, figs. 9–11 (Mogote La Resbalosa, Viñales, Cuba); holotype Museo Poey 16003, paratypes MCZ 181564.

guppyi Clench, *Omphalotropis nebulosa* 1958, Natural History of Rennell Island, British Solomon Islands, Copenhagen, Denmark, **2:** 171, pl. 17, fig. 1 (Olimbrui, Malaita, Solomon Islands); holotype AMNH 59010, paratype MCZ 93014.

Haita (subgenus) Clench & Aguayo, 1932, Proc. N.

Engl. Zool. Club, **13:** 37 (type species *Physa* [*Haita*] *elegans* Clench & Aguayo 1932, original designation).

haitiana Clench & Aguayo, *Ferrissia* (*Laevapex*) 1937, Mem. Soc. Cubana Hist. Nat., **11:**(2): 70 (Lake Miragoane, 2 mi. S of Miragoane, Haiti); holotype MCZ 83889.

haitiana Clench, *Urocoptis monilifera* 1935, Proc. Boston Soc. Nat. Hist., **41:** 2, pl. 2, fig. C (18°43′N, 72°10′W, Mirebalais road, 26 km NE of Port au Prince, Poste Terre Rouge, Haiti, ±2,000 ft.); holotype MCZ 108599.

haitiensis Clench, *Archegocoptis* 1966, Breviora, (245): 2, pl. 1, figs. 1, 2 (top of Morne Rochelois, 25 km WSW of Miragoane, Dépt. du Sud, Haiti, 3,000 ft.); holotype MCZ 252056.

hassler Clench & Aguayo, *Calliostoma* (*Astele*) 1939, Mem. Soc. Cubana Hist. Nat., **13:** 191, pl. 28, fig. 3 (*Hassler* Voyage, off Cabo Frio, Brasil, 75 mi. E of Rio de Janeiro, Brasil, 35 fth.); holotype MCZ 104554.

haysae Clench, *Thais floridana* 1927, Nautilus, **41:** 6, pl. 2, fig. 11, **44** (Grand Bayou, Mississippi Delta, Louisiana); holotype MCZ 52203, paratypes MCZ 52204.

heckerae Turner, Gustafson, Lutz & Vrijenhoek, *Bathymodiolus* 1998, Malacologia, **40**(1–2): 68, figs. 6113 (*Alvin* Dive 1343, 26°.3′N, 84°54′W, base of the W Florida Escarpment in the eastern Gulf of Mexico, 2,370 m); holotype ANSP A18846, paratype MCZ 316977 from *Alvin* Dive 1755, 26°1.5′N, 84°55.3′W, 3,300 m.

hedleyi Clench, *Isidora newcombi* 1926, J. Conch., **18:** 12 (new name for *Physa inflata* Adams and Angus 1864, non *Physa inflata* Lea 1841, non *Physa fontinalis inflata* Moquin-Tandon 1855).

helenae Clench & Turner, *Meliobba* 1960, J. Malacol. Soc. Aust., (4): 30–31, pl. 3 (5°5′S, 144°50′E, Asai-Simbai Divide, Schrader Range, a few miles due W of Aiome, Terr. of New Guinea); holotype Australian Museum C 62378 (only specimen).

helianthus Clench, *Liguus fasciatus* 1934, Occas. Pap. Boston Soc. Nat. Hist., **8:** 112, pl. 7, fig. 9 (Mogote del Palmarito, Viñales, Pinar del Rio, Cuba); holotype MCZ 80911.

hendersoni Clench, *Physa pomilia* 1925, Occas. Pap. Mus. Zool., Univ. Mich., (161): 4, pl. 1, fig. 3 (Yemassee, Beaufort Co., South Carolina); holotype UMMZ (Walker Collection no. 45640). The Walker number on the UMMZ lot corresponds to paratypes from Clench (teste Graf, personal communication). Because the holotype could not be located, these and other type lots are regarded as syntypes, UMMZ 123646, 129173; MCZ 51151.

hessei Clench & Aguayo, *Cerion* 1949, Torreira (Univ. Habana), (14): 8, pl. 1, figs. 19–22 (Balcón de las Damas, Guarda la Vaca, Banes, Cuba); holotype MCZ 183635, paratypes Museo Poey 6154.

hirasei Clench, *Bulinus* (*Culmenella*) 1927, Nautilus, **40:** 121, text fig. 1 (Prov. of Kawachi, Japan); holotype UMMZ Walker Collection no. 38964, not located in UMMZ (teste Graf, personal communication); syntypes MZUM 86896, MCZ 51425.

hispaniola Clench, *Brachypodella* (*Liparotes*) 1935, Proc. Boston Soc. Nat. Hist., **41:** 9, pl. 2, fig. F (18°22′N, 74°2′W, Tardieu, Mt. La Hotte, Pic de Macaya, 31 km SSE of Jeremie, Haiti, 3,000–4,000 ft.); holotype MCZ 108583.

hispaniolae Clench & Aguayo, *Chondropoma* (*Chondropomorus*) 1937, Mem. Soc. Cubana Hist. Nat., **11**(2): 64, pl. 7, figs. 1, 2 (Milot, Haiti); holotype MCZ 28410.

hispaniolana Clench, *Cepolis* 1964, Rev. Mus. Argent. Cienc. Nat. "Bernardino Rivadavia," **8:** 222, pl. 2, fig. 4 (Grand Cayamite Island, Haiti, Hispaniola); holotype MCZ 188262.

hoeyeri Clench, *Charopa* 1958, Natural History of Rennell Island, British Solomon Islands, Copenhagen, Denmark, **2:** 173, pl. 16, fig. 6 (Lavanggu, Rennell, Solomon Islands); holotype University Zoological Museum, Copenhagen (not numbered, teste O. S. Tendal, personal communication), paratype MCZ 191461.

holguinensis Clench & Aguayo, *Helicina* 1953 [in] Aguayo, Mem. Soc. Cubana Hist. Nat., **21:** 300, pl. 33, figs. 6, 7 (La Calera, San Germán, Holguín, Cuba); holotype Museo Poey 14311, paratypes MCZ (not received).

hoodi Clench, *Setaepoma* 1965, Breviora, (224): 4, pl. 2, fig. 3 (W side of the Tenaru River, about 0.5 mi. above the Catholic Mission, Guadalcanal, Solomon Islands); holotype MCZ 251309.

howardi Clench, *Hemitrochus* 1964, Rev. Mus. Argent. Cienc. Nat. "Bernardino Rivadavia," **8:** 223, pl. 1, fig. 5 (Monteado Nuevo, 20 km SE of Polo, Prov. de Barahona, Républica Dominicana, 4,000 ft.); holotype MCZ 187924.

howelli Clench & Aguayo, *Ficus* 1940 Mem. Soc. Cubana Hist. Nat., **14**(1): 85, pl. 14, fig. 2 (*Atlantis* Sta. 3332, 22°9′30″N, 81°11′W, Bahía de Cochinos, Santa Clara Prov., Cuba, 175–225 fth.); holotype MCZ 135140.

howelli Clench, *Liguus nobilis* 1951, Rev. Soc. Malacól. "Carlos de la Torre," **7:** 93, text fig. (Rio Dominica, about 10 mi. W of Mariel, Pinar del Rio, Cuba); holotype MCZ 187133, paratype Museo Poey 12536.

Howellia (genus) Clench & Aguayo, 1941, Mem. Soc. Cubana Hist. Nat., **15**(2): 177 (type species *Howellia mirabilis* Clench & Aguayo 1941, original designation).

hubrichti Clench, *Lithasia* 1965, Nautilus, **79:** 30, text fig. 1 (Big Black River, 3 mi. NW of Edwards, Hinds Co., Mississippi); holotype MCZ 250916, paratypes MCZ 233392.

hughesi Clench, *Cerion* 1952, Rev. Soc. Malacól. "Carlos de la Torre," **8:** 107, pl. 15, figs. 1–3 (Sand Point, Savannah Sound, Eleuthera Island, Bahamas); holotype MCZ 116026.

humberti Clench & Aguayo, *Cerion* 1949, Torreia, (14): 4, pl. 1, figs. 16–18 (Ensenada de Júcaro, Ba-

hía de Banes, Banes, Cuba); holotype MCZ 184618, paratypes Museo Poey 4266.

huntingtoni Clench, *Cerion* 1938, Bull. Mus. Comp. Zool., **80**(14): 526, pl. 3, figs. 1–3 (Colombus Point, SE tip of Cat Island, Bahamas); holotype MCZ 106956.

huntingtoni Clench, *Pupina* (*Pupina*) 1949, Bull. B. P. Bishop Mus., (196): 33, fig. 19 (N coast of Guadalcanal Island, Solomon Islands); holotype MCZ 161588, paratype Bishop Museum 190021.

icterica Bequaert & Clench, *Archachatina marginata* 1936, Rev. Zool. Bot. Afr., **29**(1): 81 (⟨Gaboon⟩); holotype MCZ 45526, only specimen.

ignava Clench & Archer, *Helicina* 1931, Occas. Pap. Boston Soc. Nat. Hist., **5:** 338, text fig. 1 (Lubang Island, Philippines); holotype MCZ 79176, paratypes MCZ 47227.

ilogana Clench & Archer, *Helicostyla* (*Chrysallis*) *mindoroensis* 1933, Pap. Mich. Acad. Sci. Arts Lett., **17:** 545, pl. 58, fig. 4 (Tara Mangyan, Abra de Ilog, Mindoro, Philippines); holotype MCZ 81359, paratypes MCZ 47264.

inaguense Clench, *Cerion* (*Diacerion*) 1933, Proc. N. Engl. Zool. Club, **13:** 98, pl. 1, fig. 9 (Northwest Pt., Gt. Inagua, Bahamas); holotype MCZ 101164.

incendium Clench, *Pseudocyclotus* 1957, Am. Mus. Novit., (1863): 2, fig. 3 (Rambutyo Island, Admiralty Islands); holotype AMNH 73486, paratypes MCZ 188140.

indianorum Clench, *Cerion paucicostatum* 1934, Proc. Boston Soc. Nat. Hist., **40**(2): 210, pl. 2, fig. F (Wemyso Biglet, Eleuthera Island, Bahama Islands); holotype MCZ 103065.

ingolfia Turner, *Xyloredo* 1972, Breviora, (397): 7, pls. 3–5 (*Ingolf* Exped. Sta. 67, 61°30′N, 22°30′W, wood dredged S of Eyrabakki, Iceland, 975 fth. [1,783 m]); holotype MCZ 279636, paratypes MCZ 279637.

insolutus Clench & Aguayo, *Opisthosiphon sainzi* 1949, Rev. Soc. Malacól. "Carlos de la Torre," **6:** 89, fig. 1 (Loma Leal, Los Haticos, Holguín, Cuba); holotype Museo Poey 12975, paratypes MCZ 167951.

insula Clench, *Brachypodella weinlandi* 1935, Proc. Boston Soc. Nat. Hist., **41:** 7, pl. 2, fig. E (Gonave Island, Haiti); holotype MCZ 106244.

Insulaceramus (subgenus) Clench, 1967, Breviora, (260): 5 (type species, *Microceramus* [*Spiroceramus*] *greenwayi* Clench 1938, original designation).

insulaefelis Clench, *Opiothosiphon bahamense* 1938, Bull. Mus. Comp. Zool., **80**(14): 515, pl. 2, figs. 1, 7 (Port Howe, southern end of Cat Island, Bahama Islands); holotype MCZ 107905.

insularis Clench, *Charopa* 1958, Natural History of Rennell Island, British Solomon Islands, Copenhagen, Denmark, **2:** 174, pl. 18, fig. 5 (Te-avamanggu, Rennell Island, Solomon Islands); holotype University Zoological Museum, Copenhagen [only specimen] (not numbered, teste O. S. Tendal, personal communication).

insularis Clench & Turner, *Truncatella thaanumi* 1948, Occas. Pap. Mollusks, **1**(13): 166 [not fig.] (near Huma, Tongatabu, Tonga Islands); holotype B. P. Bishop Museum 87796, paratypes MCZ 183889.

iselini Macdonald & Clench, *Mastigoteuthis* 1934, Occas. Pap. Boston Soc. Nat. Hist., **8:** 150, text figs. 5, 7–9 (*Atlantis* Sta. 1106, 39°4′N, 71°29′W, N Atlantic); holotype MCZ 98967.

jaumei Clench & Aguayo, *Calliostoma* (*Calliostoma*) 1946, Rev. Soc. Malacól. "Carlos de la Torre," **4:** 88, text fig. (Arenas de la Chorrera, Habana, Cuba, 3–15 fth.); holotype MCZ 178127, paratypes Museo Poey 2941.

jaumei Clench & Aguayo, *Cerion peracutum* 1953, Torreia, (18): 2, text fig. 3 (La Jijira, between Boca de Jaruco and Santa Cruz del Norte, Habana, Cuba); holotype Museo Poey 12796, paratype MCZ 187287.

jaumei Clench & Aguayo *Eutrochatella* (*Troschelviana*) 1957 [in] Aguayo, C. G., and M. L. Jaume, Mem. Soc. Cubana Hist. Nat. "Felipe Poey," **23:** 120, pl. 1, fig. 8 (Mogote de la Finca "La Esperanza" San Andrés, Consolación del Norte, Pinar de Rio, Cuba); holotype Museo Poey 13262, paratypes MCZ 212979.

jaumei Clench & Aguayo, *Jeanneretia* 1951, Rev. Soc. Malacól. "Carlos de la Torre," **7:** 87, pl. 13, figs. 14, 17 (Vega del Mamey, Pau de Guajaibon, Pinar del Rio, Cuba); holotype Museo Poey 16002, paratypes MCZ 181722.

jaumei Clench & Aguayo *Liguus blainianus* 1932, Nautilus, **45**(3): 99, pl. 6, fig. 10 (Mangas, on road between Mangas and Candelaria, Pinar del Rio, Cuba); holotype MCZ 91720.

jeanneae Clench & Turner, *Calliostoma* 1960, Johnsonia, **4:** 65, pl. 47, figs. 1, 2 (*Atlantis,* off Habana, Cuba); holotype MCZ 228370.

johnsoni Clench, *Physa* 1926, Occas. Pap. Mus. Zool., Univ. Mich., (168): 2, pl. 1, fig. 3 (Middle Spring, Hot Sulphur Springs, Banff, Alberta, Canada); holotype UMMZ 33066, paratypes MCZ 55308, 53595.

johnstoneae Clench, *Scaphella junonia* 1953, Johnsonia, **2:** 376, pl. 186, fig. 2 (off Petit Bois Island, Alabama, 10 fth.); holotype MCZ 194190.

johnstonei Clench & Turner, *Melongena corona* 1955, Johnsonia, **3**(35): 178, pl. 105, figs. 1–3 (Little Lagoon, Gulf Shores, Alabama); holotype MCZ 189687, paratypes MCZ 194022.

Jokajia Clench (subgenus) 1946, Occas. Pap. B. P. Bishop Mus., **18**(13): 204 (type species *Thaanumella* [*Jokajia*] *cookei* Clench 1946, original designation).

jonesi Clench, *Bulimulus dealbatus* 1937, Nautilus, **51**(1): 18, pl. 3, fig. 4 (2 mi. N of West Greene, Greene Co., Alabama); holotype Alabama Univ. 89, now in Florida Museum of Natural History (UF) 174304, paratype MCZ 75036.

josephi Clench & Aguayo, *Cerion* 1949, Torreia, (14):

6, pl. 1, figs. 23–25 (Playa de Uvita, al Oeste de Caletones, Gibara, Oriente, Cuba); holotype MCZ 184620, paratype MCZ 184621, paratypes Museo Poey 4264.

josephinae Clench, *Cerion* (*Strophiops*) 1935, Nautilus, **49:** 49, pl. 3, figs. 1, 4 (Tate's Bay, SE Long Island, Bahama Islands); holotype MCZ 76474.

juliae Clench, *Cerion* (*Strophiops*) 1936, Nautilus, **49**(4): 112, pl. 8, fig. 6 (Gt. Ragged Cay, SE Gt. Bahama Bank, Bahama Islands); holotype MCZ 10369.

juliae Clench, *Conus* 1942, Johnsonia, **1**(6): 26, pl. 12, fig. 4 (9 mi. off Ft. Walton, Okaloosa Co., Florida); holotype Florida Museum of Natural History (UF) 13382 [only specimen].

juliae Clench, *Helicina* 1962, Breviora, (173): 2, pl. 1, fig. 2 (Colonia Ramfis, 20 km W of San Cristobal, República Dominicana); holotype MCZ 168267.

juliae Clench & Aguayo, *Latiaxis* 1939, Mem. Soc. Cubana Hist. Nat., **13:** 194, pl. 28, fig. 4 (off Sandy Bay, Barbados, 75–100 fth.); holotype MCZ 89969.

juliae Clench, *Urocoptis* (*Autocoptis*) 1935, Proc. Boston Soc. Nat. Hist., **41:** 2, pl. 2, fig. D (Mt. Trou d'Eau, Haiti, 4,500 ft.); holotype MCZ 108601.

juliae Clench & Turner *Waghia* 1959, J. Malac. Soc. Aust., (3): 4, pl. 1, figs. 1–3, text figs.1–3 (12 mi. NE of Mt. Hagen Range, Sepik-Wahgi Divide, New Guinea, 5,000–6,000 ft.); holotype Australian Mus. C62212, paratypes MCZ 191399 and 191400.

junaluskana Clench & Banks, *Retinella* (*Glyphognomun*) 1932, Nautilus, **46:** 15, pl. 2, fig. 4 (83°47′W, 35°12′N, 2.5 mi. E of Andrews, Cherokee Co., North Carolina); holotype MCZ 86429.

juttingae Clench & Turner, *Megalacron* 1964, J. Malac. Soc. Aust., (8): 46, pl. 9, fig. 8 (3°27′S, 151°56′E, Kalili Bay, New Ireland, Bismarck Archipelago); holotype Univ. Zool. Mus., Copenhagen (not numbered, teste O. S. Tendal, personal communication), paratype MCZ 248834.

Kanapa (genus) Clench, 1949, Bull. B. P. Bishop Mus., (196): 41 (type species *Registoma torazieri* Crosse 1870, original designation).

Katastoma (section) Clench, 1935, Proc. Boston Soc. Nat. Hist., **41**(1): 8 (type species, *Brachypodella lasellensis* Clench 1935, monotypy).

katherinae Clench & Turner, *Bankia* (*Liliobankia*) 1946, Johnsonia, **2**(19): 18, pl. 11, figs. 1–6 (Bahía, Brazil); holotype MCZ 168023.

kejong Clench & Archer, *Leptopoma* 1931, Occas. Pap. Boston Soc. Nat. Hist., **5:** 337, pl. 17, fig. 6 (Lubang Island, Philippines); holotype MCZ 47224, paratypes MCZ 47225.

kieneri Clench, *Scaphella* (*Aurinia*) 1956, Johnsonia, **2:** 58 (new name for *Fusus tessellatus* Kiener, 1840 non Schubert & Wagner 1829).

kiyokoae Clench, *Kondorhaphe* 1949, Bull. B. P. Bishop Mus., (196): 28, figs. 15b, 16, 28d (Mt. Tolowan, Dublon Island, Truk Islands, Caroline Islands, 600–800 ft.); holotype Bishop Museum 9712, paratypes MCZ 140542.

klineae Clench, *Cerion* (*Maynardia*) 1961, Occas. Pap. Mollusks, **2:** 249, pl. 43, fig. 1 (Bonavista Cay, Ragged Islands, Bahama Islands); holotype MCZ 189209.

klinei Clench, *Eutrochatella* 1959, Bull. Mus. Comp. Zool., **121**(2): 34, pl. 1, fig. 5 (NE of Southwest Point, Little Inagua, Bahamas); holotype MCZ 189603.

knudseni Clench, *Quirosella* 1958, Natural History of Rennell Island, British Solomon Islands, Copenhagen, Denmark, **2:** 177, pl. 18, fig. 4, text figs. 2, 3 (Te-Avamanggu, Rennell Island, Solomon Islands); holotype University Zoological Museum, Copenhagen (not numbered, teste O. S. Tendal, personal communication), paratypes MCZ 191452, 191453.

kobelti Clench & Archer, *Pterocyclos* 1932, Occas. Pap. Boston Soc. Nat. Hist., **8:** 38, pl. 4, fig. A (Mt. Kina, Balu, North Borneo); holotype MCZ 47890, paratypes MCZ 31650.

Kombologion (subgenus) Clench & Turner, 1960, Johnsonia, **4:** 37 (type species, *Calliostoma bairdii* Verrill & Smith 1880, original designation).

kondoi Clench, *Paramia* 1945, Bull. B. P. Bishop Mus., (196): 27, figs. 15a, 28b (Nebokos, Moen Island, Truk Islands, Caroline Islands); holotype Bishop Museum 9713, paratypes MCZ 140539.

Kondorhaphe (genus) Clench, 1949, Bull. B. P. Bishop Mus., (196): 28 (type species *Kondorhaphe kiyokoae* Clench 1949, original designation).

Kubaryia (genus) Clench, 1948, Occas. Pap. B. P. Bishop Mus., **19**(8): 191 (type species *Kubaryia pilikia* Clench, 1948, original designation).

kugleri Clench & Perez Farfante, *Murex* (*Murex*) *cailleti* 1945, Johnsonia, **1**(17): 19, pl. 9, figs. 1, 2 (new name for *Murex similis* Sowerby 1841, non Schroeter 1805).

laddi Cooke & Clench, *Fijianella* 1943, Occas. Pap. B. P. Bishop Mus., **17**(20): 259, fig. 8a (Navutu Iloma, Lau Islands, Fiji Islands); holotype Bishop Museum 10108, paratypes MCZ 137109.

laddi Clench & Turner, *Taheitia turricula* 1948, Occas. Pap. Mollusks, **1**(13): 189 [not fig.] (S end of Yangasa Levu, Lau Group, Fiji Islands); holotype Bishop Museum 167165, paratypes MCZ 157850.

lahottensis Clench, *Brachypodella kraussiana* 1935, Proc. Boston Soc. Nat. Hist., **41:** 7, pl. 2, fig. I (Tardieu, Mt. La Hotte, Haiti, 3–4,000 ft.); holotype MCZ 108582.

langi Clench & Turner, *Thais* (*Thaisella*) 1948, Am. Mus. Novit., (1374): 1, figs. 7–9 (Lobito Bay, Angola, Africa); holotype AMNH 72715, paratypes MCZ 181240.

lasellensis Clench, *Brachypodella* (*Brevipodella*) 1935, Proc. Boston Soc. Nat. Hist., **41:** 8, pl. 2, fig. G (La Visite, La Selle Range, Haiti, 6–7,000 ft.); holotype MCZ 108604.

lasellensis Clench & Aguayo, *Lucidella* (*Poeniella*) 1937, Mem. Soc. Cubana Hist. Nat., **11**(2): 63, pl.

7, fig. 6 (La Visite, La Selle Range, Haiti); holotype MCZ 110626.

lauensis Clench, *Gonatorhaphe* 1949, Bull. B. P. Bishop Mus., (196): 23, fig. 10 (near Marona, Mangold, Lau Group, Fiji Islands); holotype Bishop Museum 180060 (and single broken paratype).

laureani Clench & Aguayo *Cerion* 1951, Rev. Soc. Malacól. "Carlos de la Torre," **8:** 74, pl. 11, figs. 7, 8 (Cabo Corrientes, Peninsula de Guanahacabibes South, Pinar del Rio, Cuba); holotype Museo Poey 17232, paratypes MCZ 129443, 188527, 188528.

lepidum Clench & Aguyo, *Cerion vulneratum* 1951, Rev. Soc. Malacól. "Carlos de la Torre," **8:** 76, pl. 11, figs. 10, 11 (Laguna, Punta de Mulas, Banes, Oriente, Cuba); holotype Museo Poey 12665, paratypes MCZ 166619, 178328.

Leptocalina Bequaert & Clench 1934, Rev. Zool. Bot. Afr., **26**(1): 117 (type species, *Achatina specularis* Morelet 1866, subsequent designation, Bequaert 1950, Bull. Mus. Comp. Zool., **115**[1]: 136).

lerneri Clench, *Cerion eximium* 1956, Am. Mus. Novit., (1794): 1–3, two text figs. (S tip of East Bimini, Bimini Islands, Bahamas); holotype MCZ 186830.

lewisi Clench, *Cerion* (*Multostrophia*) 1961, Occas. Pap. Mollusks, **2**(26): 255, pl. 43, fig. 5 (Pine Cay, Caicos Islands, Bahamas Islands); holotype USNM 610286, paratypes MCZ 221564.

Lignophalas (genus) Turner, 1955, Johnsonia, **3**(34): 98 (type species, *Lignophalas clappi* Turner, 1955, original designation).

Liguellus (subgenus) Clench, 1946, Occas. Pap. Mollusks, **1**(10): 123 (type species *Achatina vittata* Swainson 1822, original designation).

Liliobankia (subgenus) Clench & Turner 1946, Johnsonia, **2**(19): 17 (type species *Bankia katherinae* Clench & Turner 1946, original designation).

liliorum Clench, *Cerion* 1938, Bull. Mus. Comp. Zool., **80**(14): 527, pl. 2, figs. 2–4 (Next Point, east coast, 1.5 mi. NE of Governor's Harbour, Eleuthera Island, Bahama Islands); holotype MCZ 116086.

loveridgei Clench & Archer, *Euaethiops* 1930, Occas. Pap. Boston Soc. Nat. Hist., **5:** 298, pl. 16, fig. A (Bagilo, Uluguru Mts., Tanganyika Territory, Africa); holotype MCZ 58934, paratypes MCZ 258936.

loveridgei Bequaert & Clench, *Gonaxis* (*Macrogonaxis*) 1936, J. Conch, **20**(9): 271, text figs. 1–5 (Bagilo, Uluguru Mts., 500 ft., Tanganyika Territory, Africa); holotype MCZ 59915.

loveridgei Bequaert & Clench, *Leptocala* (*Leptocallista*) 1934, Rev. Zool. Bot. Afr., **24:** 274, pl. 1, figs. 1, 5, 6 (Nyange, 3,000 ft., Uluguru Mts., Tanganyika Territory, Africa); holotype MCZ 59949. Secondary homonym of *Achatina (Euaethiops) loveridgei* Clench & Archer 1930; renamed *Achatina arthori*. Bequaert 1950.

louisiadensis Clench, *Pupinoa* 1949, Bull. B. P. Bishop Mus., (196): 38, fig. 21C (Louisiade Islands); holotype Bishop Museum 189002, paratypes MCZ 140575.

lubanensis Clench & Archer, *Helicostyla cincinniformis* 1931, Occas. Pap. Boston Soc. Nat. Hist., **5:** 334, pl. 17, fig. 1 (Lubang Island, Philippines); holotype MCZ 79166, paratypes MCZ 79165.

lubanicus Clench & Archer, *Cyclophorus reevei* 1931, Occas. Pap. Boston Soc. Nat. Hist., **5:** 337, pl. 17, fig. 7 (Lubang Island, Philippines); holotype MCZ 47221, paratypes MCZ 47221.

lucayanorum Clench, *Cerion* (*Strophiops*) 1938, Mem. Soc. Cubana Hist. Nat., **12:** 326, pl. 25, fig. 2 (NW portion of Mores Island, 32 mi. NW of Southwest Point, Great Abaco Island, Bahamas); holotype MCZ 116017.

lucayanorus Clench, *Opisthosiphon* (*Opisthosiphon*) 1963, Bull. Mus. Comp. Zool., **128**(8): 399, pl. 3, fig. 2 (3.75 mi. NE of Salina Point, Acklins Island, Bahamas); holotype MCZ 221179.

lukolelensis Bequaert & Clench, *Maizania* (*Maizaniella*) 1936, Rev. Zool. Bot. Afr., **29**(1), p. 100, pl. 2, figs. 10, 11 (Lukolela, Belgian Congo); holotype MCZ 77206.

lymani Cl, *Conus bermudensis* 1942, Johnsonia, **1**(6): 35, pl. 13, fig. 3 (off Nellies Pt., South Lake Worth, Palm Beach Co., Florida); holotype Florida Museum of Natural History (UF) 13362 (only specimen).

macdonaldi Gustafson, Turner, Lutz & Vrijenhoek, *"Idas"* 1998, Malacologia, **40**(12): 98, figs. 11–13, 24-2 (*Johnson Sea-Link-1* Dive 3149, 27°50′N, 92°10′W, Gulf of Mexico on the Louisiana Continental Slope near Garden Banks block 386, 650 m); holotype ANSP A18850, paratypes ANSP 400783, 400784, MCZ 316980.

madaziniana Clench & Archer *Achatina* 1930, Occas. Pap. Boston Soc. Nat. Hist., **5:** 299, pl. 16, fig. B (Madazini, Tazanyika Territory); holotype MCZ 53185, paratypes MCZ 53186.

Magachatina Bequaert & Clench 1936, Rev. Zool. Bot. Afr., **29**(l): 78, misspelling of *Megachatina.*

magnifica Boss & Turner, *Calyptogena* 1980, Malacologia, **20**(1): 161, figs. 1–9, 10F–G, 11, 12D–F, 13 (*Alvin* Dive 717, 0°47.9′N, 86°8.5′W, Galapagos Rift, 2,459 m); holotype MCZ 288500.

Maizaniella (subgenus) Bequaert & Clench, 1936, Rev. Zool. Bot. Afr., **29**(1): 99 (type species, *Cyclophorus leonensis* Morelet 1873, original designation).

Malaitella Clench, 1941, Am. Mus. Novit., (1129): 11 (new name for *Acrotylus* Clench 1935, non Cossmann 1896).

malaitensis Clench, *Placostylus* (*Malaitella*) 1941, Am. Mus. Novit., (1129): 11, fig. 4 (near Su'u, Malaita Island, Solomon Islands); holotype AMNH 79006, paratype MCZ 92905, Aola Mulaita Island, 3,000 ft.

malonei Clench, *Cerion* 1937, Nautilus, **51:** 30, pl. 3, fig. 6 (3.5 mi. SE of Simms, Long Island, Bahamas); holotype MCZ 112706.

mamburaoensis Clench & Archer, *Obba planulata* 1932, Occas. Pap. Boston Soc. Nat. Hist., **8:** 40, pl.

4, fig. D (Calomintao, Mamburao, Mindoro, Philippines); holotype MCZ 92799.

manni Clench & Aguayo, *Chondropoma* (*Chondropomorus*) 1937, Mem. Soc. Cubana Hist. Nat., **11**(2): 65, pl. 7, fig. 3 (Furcy, Haiti); holotype MCZ 25415, paratype MCZ 36692.

manni Clench, *Kanapa* 1949, Bull. B. P. Bishop Mus., (196): 42, figs. 23a–24b–d MCZ (Three Sisters Islands, Solomon Islands); holotype MCZ 141012, paratypes Bishop Museum 188844.

manni Clench & Aguayo, *Lucidella* 1932, Proc. N. Engl. Zool. Club, **13:** 35 (Furcy, Haiti); holotype MCZ 23414.

marcanoi Clench, *Proserpina* 1962, Breviora, (173): 2, pl. 1, fig. 3 (Colonia Ramfis, 20 km W of San Cristobal, República Dominicana); holotype MCZ 188911.

mariae Clench, *Liguus fasciatus* 1935, Nautilus, **48:** 123, pl. 7, fig. 3 (Ojo de Agua, near Cayo Magueyal, Pinar del Rio, Cuba); holotype MCZ 94224.

maricao Clench, *Polydontes* (*Granodormus*) 1940, Mem. Soc. Cubana Hist. Nat., **14**(3): 243, pl. 42, figs. 2, 5 (Maricao Forest, 2–3,000 ft., W Puerto Rico); holotype MCZ 111636.

mariguanense Clench, *Cerion* (*Strophiops*) 1933, Proc. N. Engl. Zool. Club, **13:** 94, pl. 1, fig. 3 (S coast of Mariguana Island, Bahamas); holotype MCZ 101162.

mariguanense Clench, *Chondropoma* 1937, Proc. N. Engl. Zool. Club, **16:** 66, pl. 3, fig. 2 (Abrahams Hill, 2 mi. NE of Abrahams Bay, Mariguana Island, Bahamas); holotype MCZ 57987.

matthewsae Clench & Turner, *Epitonium multistriatum* 1952, Johnsonia, **2:** 295, pl. 135 (Sanibel Island, Florida); holotype MCZ 197134.

mauritii Bequaert & Clench, *Volvatorbis* 1936, Mem. Mus. R. Hist. Nat. Belg., 2nd ser., (3): 166, fig. 2 (Ango-Ango, 4 km S of Matadi, Congo River, Belgian Congo); holotype MCZ 59803.

maya Bequaert & Clench, *Spiraxis* (*Volutaxis*) 1931, Occas. Pap. Boston Soc. Nat. Hist., **5:** 423 (Chichenltza, Yucatan); holotype MCZ 85799.

mayabigensis Clench & Archer, *Obba listeri* 1932, Occas. Pap. Boston Soc. Nat. Hist., **8:** 39, pl. 4, fig. C (Mayabig, Baco, Mindoro, Philippines); holotype MCZ 92798, paratypes MCZ 93992.

mayri Clench, *Palaeohelicina* (*Palaeohelicina*) 1958, Natural History of Rennell Island, British Solomon Islands, Copenhagen, Denmark, **2:** 163, pl. 1, fig. 7 (Auki, Malaita, Solomon Islands); holotype MCZ 32610.

mayri Clench, *Placostylus* (*Aspastus*) *miltocheilus* 1941, Am. Mus. Novit., (1129): 19 (new name for *Bulimus (Aspastus) miltocheilus minor* Brazier 1894 non Kobelt 1891).

mayri Clench, *Setaepoma* 1958, Natural History of Rennell Islands, British Solomon Islands, Copenhagen, Denmark, **2:** 168, pl. 17, fig. 5, text fig. 1 (Fulakora, Ysebel, Solomon Islands); holotype MCZ 36840.

mcgintyi Clench, *Liguus fasciatus* 1934, Occas. Pap. Boston Soc. Nat. Hist., **8:** 116, pl. 7, fig. 10 (Cueva del Chivo, Mariel, Pinar del Rio, Cuba); holotype MCZ 47384.

mcleani Clench, *Alcadia* (*Alcadia*) 1937, Proc. N. Engl. Zool. Club, **16:** 74, pl. 3, fig. 6 (Landrail Point, Crooked Island, Bahamas); holotype MCZ 64782.

mcleani Clench, *Cerion* 1937, Nautilus, **51:** 22, pl. 3, fig. 7 (1 mi. E of O'Neills, Long Island, Bahamas); holotype MCZ 112701.

mcleani Clench, *Polydontes* (*Hispaniolana*) 1964, Rev. Mus. Argent. Cienc. Nat. "Bernardino Rivadavia," **8:** 217, pl. 2, fig. 1 (below Valle Nuevo, SE of Constanza, Prov. de la Vega, Républica Dominicana); holotype MCZ 188213.

mcleani Clench, *Trochomorpha* 1958, Natural History of Rennell Island, British Solomon Islands, Copenhagen, Denmark, **2:** 179, pl. 17, fig. 6 (10 mi. inland from Su'u, Malaita Island, Solomon Islands); holotype AMNH 79016, paratype MCZ 93070.

Mcleani (genus) Bequaert & Clench, 1939, Mem. Soc. Cubana Hist. Nat., **13:** 283 (type species *M. darlingtoni* Bequaert & Clench 1939, original designation).

mcmichaeli Clench & Turner *Elliptio* 1956, Bull. Fla. State Mus., **1**(3): 170, pl. 7, figs. 1, 2 (Chactawhatchee River, 8 mi. W of Miller Cross Roads, Holmes Co., Florida); holotype MCZ 191922.

mcmichaeli Clench & Turner, *Meliobba* 1963, J. Malacol. Soc. Aust., (6): 24, pl. 2, fig. 3, text figs. 3(2), 6(4), 7 (Noorweg, Hollandia, Dutch New Guinea); holotype Aust. Museum C. 62377, paratype MCZ 87618.

mcmurrayi Clench & Aguayo, *Latirus* (*Hemipolygona*) 1941, Mem. Soc. Cubana Hist. Nat., **15:** 178, pl. 14, fig. 3 (*Atlantis* Sta. 3482, 23°9′N, 81°27′30″W, off Matánzas, Cuba, 190 fth.); holotype MCZ 135285.

Megachatina (subgenus) Bequaert & Clench 1926, Rev. Zool. Bot. Afr., **29**(1): 76 (type species *Achatina marginata* Swainson 1821, original designation).

Megachatinops Bequaert & Clench, 1936, Rev. Zool. Bot. Afr., **29**(1): 87, misspelling of *Megachatinopsis.*

Megachatinopsis (subgenus) Bequaert & Clench, 1936, Rev. Zool. Bot. Afr., **29**(1): 76 (type species, *Achatina knorrii* Jonas 1839, original designation).

melanesia Clench & Turner, *Megalacron* 1964, J. Malac. Soc. Aust., **8:** 53, pl. 10, fig. 14, text fig. 5 (waterfall, Lorengau, Manus Island, Admiralty Islands, Bismarck Archipelago); holotype University Museum, Copenhagen (not numbered, teste O. S. Tendal, personal communication), paratypes MCZ 249306.

melanostomum Clench, *Cerion* (*Strophiops*) 1934, Proc. Boston Soc. Nat. Hist., **40**(2): 212, pl. 2, figs. A, C (Mortimer's, S end of Long Island [Berry Island], Bahama Islands); holotype MCZ 103021.

Merrilliana (subgenus) Clench & Turner, 1948, Oc-

cas. Pap. Mollusks, **1**(13): 179 (type species, *Truncatela elegans* C. B. Adams 1849, original designation).

Mesanella (genus) Clench & Turner, 1952, Nautilus, **66:** 32 (type species, *Helix trailli* Pfeiffer 1855, original designation).

michiganensis Clench, *Physa* 1926, Occas. Pap. Mus. Zool., Univ. Mich., (168): 4, pl. 1, fig. 4 (stream 1 mi. W of Geddes, Washtenau Co., Michigan); holotype UMMZ 33068, paratypes MCZ 251177.

mirabilis Clench & Aguayo, *Howellia* 1941, Mem. Soc. Cubana Hist. Nat., **15**(2): 177, pl. 14, fig. 2 (*Atlantis* Sta. 3483, 23°12′N, 81°23′W, off Matánzas, Cuba, 285 fth.); holotype MCZ 135291.

modica Clench & Aguayo *Jeanneretia* (*Guladentia*) 1951, Rev. Soc. Malacól. "Carlos de la Torre," **7:** 89, pl. 14, figs. 7, 8 (Mal Paso, Luis Lazo, Pinar del Rio, Cuba); holotype Museo Poey 17220, paratypes MCZ 181560 from Le Caoba, Luis Lazo, Cuba.

monactia Clench & Archer, *Helicostyla* (*Calocochlea*) 1933, Pap. Mich. Acad. Sci. Arts Lett., **17:** 539, pl. 57, fig. 1 (Binuangan, Palúan, Mindoro, Philippines); holotype MCZ 81353.

monaense Clench, *Cerion* 1951, J. Conchy., **90:** 274, figs. 7–11 (Mona Island, Puerto Rico); holotype MCZ 171019.

montana Clench, *Coryda* 1964, Rev. Mus. Argent. Cienc. Nat. "Bernardino Rivadavia," **8:** 226, pl. 2, fig. 5 (Loma Vieja, SW of Constanza, Prov. de la Vega, Républica Dominicana); holotype MCZ 187954.

montana Clench, *Polydontes* (*Hispaniolana*) 1964, Rev. Mus. Argent. Cienc. Nat. "Bernardino Rivadavia," **8:** 216, pl. 2, fig. 2 (Mt. Quita Espuela, 14 km NE of San Francisco de Macoris, Prov. Duarte, Républica Dominicana); holotype MCZ 188209.

monticola Clench & Archer, *Thersites* 1938, J. Conch., **21:** 22, pl. 1, fig. 4 (Mt. Spurgeon, 50 mi. NW of Cairns, Queensland); holotype MCZ 99053, paratypes Queensland Museum, South Brisbane, Queensland (QMMO) 1764.

moralesi Clench & Aguayo, *Cerion torrei* 1951, Rev. Soc. Malacól. "Carlos de la Torre," **8:** 77, pl. 11, figs. 13, 14 (Playa de Morales, 11 km SE of Banes, Oriente, Cuba); holotype Museo Poey 17293, paratypes MCZ 187476.

moreleti Clench & Aguayo, *Cerion iostomum* 1951, Rev. Soc. Malacól. "Carlos de la Torre," **8:** 73, pl. 11, fig. 6 (Punta del Este, Isle of Pines, Cuba); holotype Museo Poey 17249, paratypes MCZ 129129, 188542.

moseleyae Clench, *Hojeda* 1938, Mem. Soc. Cubana Hist. Nat., **12:** 324, pl. 24, figs. 4, 5 (Eight Mile Rock, Grand Bahama Island, Bahamas); holotype MCZ 116738.

mossi Clench, *Cerion* 1952, Rev. Soc. Malacól. "Carlos de la Torre," **8:** 108 (new name for *Cerion paucicostatum* Clench 1934, non Torre 1929).

moussoni Clench, *Melanoides tuberculata* 1927, Nautilus, **40:** 101 (new name for *Melania tuberculata plicifera* Mousson 1849, non *Melania plicifera* Lea 1839).

mukongo Bequaert & Clench, *Subulina* (*Nothapalus*) *paucipira* 1941, Bull. Mus. Comp. Zool., **88:** 11, pl. 2, figs. 6–8 (Luadi-Soyo, near Neatadi, Belgian Congo); holotype MCZ 112302.

muraokai Turner, *Xylophaga* 2002, Bull. Mus. Comp. Zool., **157**(4): 247, pls. 18, 19 (30° 44′N, 120° 45′W, about 81 mi. SW of Port Hueneme, California, or about 25 mi. S of San Miguel Island, Santa Barbara Islands, 1,720 m); holotype MCZ 316746, paratypes MCZ 316747–50.

Murexiella (subgenus) Clench & Perez Farfante 1945, Johnsonia, (17): 49 (type species, *Murex hidalgoi* Crosse 1896, original designation).

murilloi Clench, *Musculium* 1939, Mem. Soc. Cubana Hist. Nat., **13**(5): 286, pl. 36, fig. 1 (Soacha, Dept. Cundinamarea, Columbia); holotype MCZ 91374, paratypes MCZ 91373; paratypes MCZ 91375 from Fugene, 82 km N of Bogota, Dept. Cundinamarea, 2,430 m.

naceli Turner, *Xyloredo* 1972, Breviora, (397): 9, pl. 6 (U.S. Naval Civil Eng. Lab STU 1–4, 33°46′N, 120°46′W, about 30 mi. S of San Miguel Island, off Port Hueneme, California, 2,072.6 m); holotype MCZ 279638, paratypes MCZ 279639.

nairi Turner & Santhakumaran, *Martesia* (*Particoma*) 1989, Ophelia, **30**(3): 163, figs. 7–10 (Neendakara, stamudi estuary, 7 km N of Quilon, Keraka, India); holotype MCZ 298201, paratypes MCZ 297202.

najazaensis Cl & Jacobson, *Troschelviana pfeifferiana* 1971, Bull. Mus. Comp. Zool., **141**(7): 440, pl. 4, fig. 8 (El Cacaotal, Najaza, Camagüey, Cuba); holotype MCZ 92091, paratypes MCZ 127517, 273217.

najazensis Clench & Aguayo Caracolus 1951, Mem. Soc. Cubana Hist. Nat., **20:** 69, pl. 41, figs. 9–11 (El Cacaotal, Najaza, Camagüey, Cuba); holotype Museo Poey 17304, paratypes MCZ 181501.

nantahala Clench & Banks, *Polygyra* (*Triodopsis*) 1932, Nautilus, **46:** 17, pl. 2, figs. 1, 2, 5 (35°38′N, 83°39′W, Blowing Springs, Cliff Ridge, Nautahala Gorge, Swain Co., North Carolina); holotype MCZ 86429.

nanus Clench & Aguayo, *Cadulus* (*Gadila*) *iota* 1939, Mem. Soc. Cubana Hist. Nat., **13:** 197 (not fig.) (Gibara, Cuba, 40 fth.); holotype MCZ 89222.

naufraga Clench, *Leptinaria Abaconia* 1938, Mem. Soc. Cubana Hist., **12:** 321, pl. 24, figs. 1, 2 (Sand Bank, Crossing Bay, Gt. Abaco Island, Bahamas); holotype MCZ 116705.

neptunia Clench & Aguayo, *Aurinia* 1940, Mem. Soc. Cubana Hist. Nat., **14:** 90, pl. 16, fig. 5 (*Blake* Sta. no. 8, 17°45′N, 77°58′40″W, off Banner Reef, Pedro Bank, 75 mi. S of Jamaica, 322 fth.); holotype MCZ 119025.

Nesopoma (genus) Clench, 1958, Natural History of Rennell Island, British Solomon Islands, Copenhagen, Denmark, **2:** 169 (type species, *Nesopoma eyerdami* Clench 1958, original designation).

neztalia Turner & McKoy, *Bankia* 1979, J. R. Soc. N. Z., **9**(4): 465, figs. 2–9, 17–31 (Wellington Harbor, New Zealand); holotype MCZ 280345.

nioba Clench & McLean, *Macrocallista* (*Paradione*) 1936, J. Conch., **20:** 201 (new name for *Venus costata* Chemnitz 1795, non Gmelin 1791).

nobilis Clench & Aguayo, *Liguus fasciatus* 1932, Nautilus, **45**(3): 98, pl. 6, fig. 9 (Cayo Juan Tomas, mouth of Cabanas Bay, Pinar del Rio, Cuba); holotype MCZ 47904.

nodali Clench & Aguayo, *Cerion disforme* 1953 [in] Aguayo, Mem. Soc. Cubana Hist. Nat., **21:** 310, pl. 35, fig. 6 (El Cañonde Banes, cerca del Faro, Oriente, Cuba); holotype Museo Poey 121404, paratypes MCZ (not received).

nooi Turner *Xyloredo* 1972, Breviora, (397): 5, pls. 1, 2 (250 54′N, 77°49′W, from test panel, Tongue of the Ocean, off Andros Island, Bahamas, 1,737 m); holotype MCZ 279631, paratypes MCZ 279832–5.

norvegicum Clench & Turner, *Epitonium greenlandicum* 1952, Johnsonia, **2**(31): 323, pl. 155, fig. 1 (new name for *Scalaria groenlandica ornata* Friele & Grieg 1901, non *S. ornata* Baily 1865).

Nystiella (genus) Clench & Turner, 1952, Johnsonia, **2**(31): 337 (type species, *Epitonium opalinum* Dall 1927, original designation).

Nystiellinae (subfamily) Clench & Turner, 1952, Johnsonia, **2**(31): 337 (type species, *Epitonium opalinum* Dall 1927, original designation).

obesum 'Torre' Clench & Aguayo, *Cerion* 1951, Rev. Soc. Malacól. "Carlos de la Torre," **8:** 80 ([nomen nudem] listed as a synonym under *Cerion pauicostatum* Torre).

occidentale Clench & Turner, *Cymatium* (*Septa*) *rubeculum* 1957, Johnsonia, **3:** 214, pl. 110, fig. 3; pl. 113, fig. 5; pl. 121, figs. 1–3 (St. Thomas, Virgin Islands); holotype ANSP 36874, paratype MCZ 202269 from Carboneras, Matánzas, Cuba.

occidentalis Clench & Archer, *Cyclophorus fernandezi* 1932, Occas. Pap. Boston Soc. Nat. Hist., **8:** 37, pl. 4, fig. B (Calominatao, Mamburao, Mindoro, Philippines Islands); holotype MCZ 92797, paratypes MCZ 93841.

Odontocymbiola Clench & Turner, 1964, Johnsonia, **4:** 170 (new name for *Adelomelon* 'Dall' Pilsbry & Olsson 1954, non Dall 1906).

Odontocymbiolinae Clench & Turner, 1964, Johnsonia, **4:** 170 (new name for *Adelomeloninae* based upon *Adelomelon* Pilsbry & Olsson 1954, non Dall 1906).

ophir Clench, *Placostylus* (*Malaitella*) 1941, Am. Mus. Novit., (1129): 11, fig. 9 (20 mi. inland from Su'u, Malaita Island, Solomon Islands); holotype AMNH 79005, paratypes MCZ 92902, 92904 from Aurola, Malaita Island.

oregon Clench & Turner, *Calliostoma* (*Kombologion*) 1960, Johnsonia, **4:** 42, pl. 2; pl. 6, fig. 2; pl. 27 (*Oregon* Sta. 5501, 26°55′N, 96°25′W, about 70 mi. SE of Corpus Christi, Texas, 125 fth.); holotype USNM 612705, paratype MCZ 235480.

organensis Clench, *Liguus flammellus* 1934, Occas. Pap. Boston Soc. Nat. Hist., **8:** 124, pl. 6, fig. 8 (Eusenada del Valle, Viñales, Pinar del Rio, Cuba); holotype MCZ 80958.

orientale Clench & Aguayo, *Cerion* 1951, Rev. Soc. Malacól. "Carlos de la Torre," **8:** 79, pl. 11, fig. 16 (Punta Nigra, 18 km SW of Punta Maisi, Oriente, Cuba); holotype Museo Poey 12534, paratypes MCZ 188582.

orites Cooke & Clench, *Electrina succinea* 1943, Occas. Pap. B. P. Bishop Mus., **17**(20): 252, fig. 2 (eastern Ridge of Mt. Perahu, Rapa Island, Central Pacific, 1,300–1,550 ft.); holotype Bishop Museum 10111, paratypes MCZ 144791.

orotis Clench & Archer, *Helicostyla mindoroensis* (*Chrysallis*) 1933, Pap. Mich. Acad. Sci. Arts Lett., **17:** 549, pl. 58, fig. 1 (near Calavite Mt., Binuangan, Palúan, Mindoro, Philippines); holotype MCZ 81360.

orrae Turner, *Taheitia* 1959, Occas. Pap. Mollusks, **2**(23): 186, pls. 31, 32 (sink-hole cave behind air strip, Biak, Dutch New Guinea); holotype ANSP 223656, paratypes MCZ 221170.

osmenti Clench, *Drymaeus multilineatus* 1948, Nautilus, **62:** 36 (Little Pine Key, Lower Florida Keys); holotype MCZ 160807.

osmenti Clench, *Liguus fasciatus* 1942, Proc. N. Engl. Zool. Club, **19:** 69 (Howes Key, Lower Florida Keys); holotype MCZ 137792.

ottenwalderi Wetherbee & Clench, *Macroceramus* 1984, Caribb. J. Sci., **20**(1–2): 11, fig. 1, pl. 1, pt. C, right side (Mt. Isabel de Torres, Puerto Plata Prov., República Dominicana); holotype MCZ 57490 (rightmost figure), paratypes MCZ 57491.

pallidior Bequaert & Clench, *Pseudogibbula duponti* 1941, Bull. Mus. Comp. Zool., **88**(1): 7 [not fig.] (Matadi, Congo River, Belgian Congo); holotype MCZ 112265.

palmeri Clench & Rehder, *Humboldtiana* 1930, Nautilus, **44:** 12, pl. 2, figs. 1–4 (head of Madera Canyon, 7,350 ft., Mt. Livermore, Davis Mts., Jeff Davis Co., Texas); holotype MCZ 79779.

pandion Clench & Turner, *Epitonium* (*Boreoscala*) 1952, Johnsonia, **2:** 326, pl. 157 (new name for *Acirsa gracilis* Verrill 1880, non *Scalaria gracilis* Sowerby, 1844).

Papuanella (genus) Clench & Turner, 1959, J. Malacol. Soc. Aust., (3): 5 (type species *Geotrochus ogeramuensis* Kobelt 1914, original designation).

parallaxis Clench & Archer, *Helicostylus mindoroensis* (*Chrysallis*) 1933, Pap. Mich. Acad. Sci. Arts Lett., **17:** 550, pl. 518, fig. 2 (Palúan, Mindoro, Philippines); holotype MCZ 83275.

Paramia (genus) Clench 1949, Bull. B. P. Bishop Mus., (196): 25 (type species, *Cyclostoma incisa* Hombron & Jacquinot 1854, original designation).

Paramiella Clench, 1954, Nautilus, **67:** 139 (new name for *Paramia* Clench 1949, non Bleeker 1863).

paravicinii Clench, *Partula* 1933, Nautilus, **47:** 24, pl.

3, figs. 5, 6 (St. Matthias, Bismarck Archipelago); holotype MCZ 59854.

parvulina Clench & Turner, *Geomelania* (*Merrilliana*) 1948, Occas. Pap. Mollusks, **1**(13): 180 (new name for *Geomelania parva* Chitty 1853, non *parva* C. B. Adams 1850).

pattersoni Clench, *Oliva reticularis* 1945, Mollusca, **1**(4): 49, figs. 1, 2 on pl. (5 mi. E of Crabbing Point, Grand Bahama Island, Bahamas); holotype MCZ 151166.

paucicostatum Clench, *Cerion* (*Strophiops*) 1934, Proc. Boston Soc. Nat. Hist., **40**(2): 209, pl. 2, fig. E (Miller's Hill, southern Eleuthera, Bahama Islands); holotype MCZ 103033.

pauciculptum Clench & Aguayo, *Cerion* (*Umbonis*) 1952, Occas. Pap. Mollusks, **1**(17): 425, pl. 54, figs. 1–2 (Punta de Musica, Bahía de Samá, Banes, Cuba); holotype MCZ 192204.

peracutum Clench & Aguayo, *Cerion sagraianum* 1951, Rev. Soc. Malacól. "Carlos de la Torre," **8:** 75, pl. 11, fig. 9 (Boca de Jaruco, Habana Prov., Cuba); holotype Museo Poey 17268, paratype MCZ 187285, 188533.

periculosum Clench, *Cerion* (*Strophiops*) 1934, Proc. Boston Soc. Nat. Hist., **40**(2): 215, pl. 2, fig. B (South Cay, Mira Por Vos Group, Bahama Islands); holotype MCZ 103019.

perryae Clench, *Conus* 1942, Johnsonia, **1**(6): 31, pl. 15, fig. 5 (6 mi. off Sanibel Island, Lee Co., Florida); holotype MCZ 206055.

pescalia Clench & Turner, *Odontocymbiola* 1964, Johnsonia, **4:** 172, pls. 110, 111 (about 160 mi. ENE of Mar del Plata, Argentina, on a mud bottom); holotype MCZ 233795.

pihapilia Clench, *Ponapella* 1946, Occas. Pap. B. P. Bishop Mus., **18:** 200, text fig. 1 (Mt. Tolotom, Ponape, Caroline Islands); holotype Bishop Museum 189003, paratypes & MCZ 140577.

pilikia Clench, *Kubaryia* 1948, Occas. Pap. B. P. Bishop Mus., **19**(8): 191, figs. 1a–d (Komakau, Koror Island, Palau Islands, Caroline Islands); holotype Bishop Museum 158887 (only specimen).

pilsbryi Clench, *Goodrichia trochiformis* 1929, Bull. Mus. Comp. Zool., **69:** 119, pl. 1, figs. 5, 6 (Sakbayeme, Cameroon); holotype MCZ 78073, paratypes MCZ 78067.

pilsbryi Bequaert & Clench, *Gubella* 1936, Nautilus, **49:** 95, pl. 6, figs. 5–7 (Liberia); holotype ANSP 23891, paratype MCZ 106384.

pilsbryi Clench, *Liguus blainianus* 1935, Nautilus, **48:** 123, pl. 7, fig. 1 (Campo de Tiro, 7 km N of Fierro, Pinar del Rio, Cuba, near Santa Cruz de los Pinos); holotype MCZ 94212.

pilsbryi Clench, *Macroceramus* 1935, Proc. Boston Soc. Nat. Hist., **41:** 11, pl. 1, fig. J (Camp Perrin, Haiti); holotype MCZ 108605.

pilsbryi Clench, *Spiroceramus* (*Spiroceramus*) 1967, Breviora Mus. Comp. Zool., (26): 4, pl. 1 (Cerro de Tuabagüey, Sierra de Cubítas, Camagüey Prov., Cuba); holotype MCZ 188845, paratypes MCZ 188847, 256082.

pinarensis Clench, *Liguus fasciatus* 1934, Occas. Pap. Boston Soc. Nat. Hist., **8:** 115, pl. 6, fig. 9 (Punta del Este, Isle of Pines, Cuba); holotype MCZ 58806.

piratica Clench & Aguayo, *Bathyaurinia* 1940, Mem. Soc. Cubana Hist. Nat., **14:** 93, pl. 15, fig. 2 (*Atlantis* Sta. 2982A, 22°48′N, 78°50′W, off Punta Alegre, Camagüey Prov., Cuba, 210 fth.); holotype MCZ 135235.

piratica Clench & Turner, *Truncatella scalaris* 1948, Johnsonia, **2:** 161, pl. 72, figs. 1–4 (St. George's Causeway, Bermuda); holotype MCZ 178985.

piraticus Clench, *Cerion* (*Strophiops*) 1937, Proc. N. Engl. Zool. Club, **16:** 64, pl. 3, fig. 1 (Southeast Point, 12 mi. SE of Abrahams Bay, Mariguana Island, Bahamas); holotype MCZ 57926.

piraticus Clench, *Conus verrucosus* 1942, Johnsonia, (6): 14, pl. 11, fig. 1 (off Palm Beach, Florida); holotype McGinty collection, now in Florida Museum of Natural History (UF) 174328, paratype MCZ 145458, from Carysfort Reef, Florida, 10 fth.

platei Clench, *Cerion* (*Strophiops*) 1933, Proc. N. Engl. Zool. Club, **13:** 90, pl. 1, figs. 7, 8 (Bight road, Cat Island, Bahamas); holotype MCZ 95731.

plena Bequaert & Clench, *Hydrobia* 1936, Mem. Mus. R. Hist. Nat. Belg., 2nd ser., (3): 165, pl. 1, fig. 5 (Ango-Ango, 4 km S of Congo River, Belgian Congo); holotype MCZ 59802 (only specimen).

plena Clench, *Physa* 1930, Occas. Pap. Boston Soc. Nat. Hist., **5:** 311, text fig. 3 (Reed Spring, Centerville, Reynolds Co., Missouri); holotype MCZ 51850, paratypes MCZ 51851.

Plesiophysinae (subfamily) Bequaert & Clench, 1939, J. Conch., **21:** 175 (type genus *Plesiophysa* P. Fischer 1883).

Plumulella (subgenus) Clench & Turner, 1946, Johnsonia, **2**(19): 22 (type species *Teredo fimbriata* Jeffreys 1860 [=*Bankia fimbriatula* Moll and Roch 1931], original designation).

polinigi Clench, *Eustomopsis* (*Verdichloritis*) 1957, Breviora, (76): 1, fig. 1 (Western New Guinea); holotype MCZ 212319.

Ponapella (genus) Clench, 1946, Occas. Pap. B. P. Bishop Mus., **18**(13): 199 (type species, *Ponapella pihapiha* Clench 1946, original designation).

ponapensis Clench, *Thaanumella cookei* 1946, Occas. Pap. B. P. Bishop Mus., **18**(13): 205 (Mt. Tolotom, Ponape, Caroline Islands, 800 ft.); holotype Bishop Museum 154096 (only specimen).

popondetta Clench & Turner, *Meliobba* 1963, J. Malacol. Soc. Aust., (6): 26, pl. 2, fig. 1, text figs. 3(3), 6(3), 8 (Mamoo Estate, Near Popondetta, about 12 mi. S of Buna, Papua, New Guinea); holotype Australian Museum C 62376, paratype MCZ 221417.

porphyrotoma Clench & Archer, *Strophocheilus* (*Strophocheilus*) 1930, Nautilus, **43**(3): 75, text figs. 1–3 (mountain near Jacquaral, Sao Paulo, Brazil); holotype MCZ 79108.

pourtalesi Clench & Aguayo, *Solariella* 1939, Mem. Soc. Cubana Hist. Nat., **13:** 190, pl. 28, fig. 2 (*At-*

lantis Sta. 2993, 23°24′N, 80°44′W, off Cardenas, N Cuba, 580 fth.); holotype MCZ 135108.

prashadi Clench, *Camptoceros* (*Culmenella*) 1931, Nautilus, **44**(3): 80 (new name for *Bulimus* [*Culmenella*] *hirasei* Clench 1927, non *Camptocerus hirasei* Walker 1919).

prasinata Jacobson & Clench, *Helicina* 1971, Nautilus, **84**(3): 105, text fig. 1 (Monteado, Nuevo 20 km SE of Polo, Barahona Prov., Dominican Republic); holotype MCZ 187927.

Proaspastus (subgenus) Clench, 1941, Am. Mus. Novit., (1129): 12 (type species, *Bulimus sanchristovalensis* Cox 1870, original designation).

profunda Turner, *Xylophaga* 2002, Bull. Mus. Comp. Zool., **157**(4): 243, pls. 12, 13 (25°54′N, 77°49′W, Tongue of the Ocean, off NE tip of Andros Island, Bahama Islands, 1,722 m); holotype MCZ 316751.

pterinus Clench & Archer, *Thersites* 1938, J. Conch., **21:** 21, pl. 1, fig. 3 (Lake Barrine, 25 mi. SW of Cairns, Queensland); holotype Queensland Museum, South Brisbane, Queensland, QMMO 1769, paratype UMMZ from Lake Eacham, close to Lake Barraine.

Pupina (genus) Clench, 1949, Bull. B. P. Bishop Mus., (196): 37 (type species, *Pupina aurea* Hinds 1842, original designation).

Pupinesia (genus) Clench, 1949, Bull. B. P. Bishop Mus., (196): 39 (type species, *Pupina adamsiana* Crosse 1871, original designation).

quillingi Turner, *Jouanuetia* (*Pholadopsis*) 1955, Johnsonia, **3**(34): 139, pl. 84 (N end of Lake Worth Inlet, Lake Worth, Florida); holotype MCZ 189913.

quiñonesi Clench & Aguayo, *Alcadia* 1950, Rev. Soc. Malacól. "Carlos de la Torre," **7:** 63, pl. 12, figs. 9–11 (Los Tambores, entre Playa Puerto Rico y Punta de Mulas, Banes, Oriente, Cuba); holotype Museo Poey 12913, paratypes MCZ 185800.

quiñonesi Clench & Aguayo, *Cepolis* (*Coryda*) *alauda* 1957 [in] Aguayo, C. G., and M. L. Jaume, Mem. Soc. Cubana Hist. Nat. "Felipe Poey," **23:** 130, pl. 4, figs. 4–6 (coast between Morales and el Cañon, Banes, Oriente, Cuba); holotype Museo Poey 15097, paratypes MCZ 212977.

Quirosella (genus) Clench, 1958, Natural History of Rennell Island, British Solomon Islands, Copenhagen, Denmark, **2**(27): 175 (type species, *Quirosella coultasi* Clench 1958, original designation).

quirosi Clench, *Ompahlotropis* 1958, Natural History of Rennell Island, British Solomon Islands, Copenhagen, Denmark, **2**(27): 171, pl. 17, fig. 3 (Lavanggu, Rennell, Solomon Islands); holotype University Zoological Museum, Copenhagen (not numbered teste O. S. Tendal, personal communication); paratypes MCZ 191443.

randi Clench, *Zaphysema* 1962, Breviora, (173): 4, pl. 1, fig. 1 (Cueva de San Francisco, Cerros de San Francisco, Mun. Pedro Santana, San Rafael, República Dominicana); holotype MCZ 230503, paratype MCZ 320504.

Rapanella (genus) Cooke & Clench, 1943, Occas. Pap. B. P. Bishop Mus., **17**(20): 253 (type species, *Rapanella andersoni* Cooke & Clench, monotypy).

rehderi Clench & Aguayo, *Cerion* (*Umbonis*) 1943, Occas. Pap. Mollusks, **1**(17): 422, pl. 57, fig. 2 (Jackline, 1 mi. W of Conch Shell Point, Gt. Inagua, Bahama Islands); holotype MCZ 189032.

Rehderia (genus) Clench, 1946, Johnsonia, **2**(27): 45 (type species *Aurinia schmitti* Bartsch 1931, original designation).

remingtoni Clench, *Physa* 1930, Occas. Pap. Boston Soc. Nat. Hist., **5:** 312, text fig. 4 (Round Spring, 12 mi. N of Eminence, Shannon Co., Missouri); holotype UMMZ 32663, paratypes MCZ 50984.

rennellensis Clench, *Crystallopsis* (*Cristovala*) 1958, Natural History of Rennell Island, British Solomon Islands, Copenhagen, Denmark, **2:** 190, pl. 16, fig. 2, text figs. 2, 3 (Te-avamangga, Rennell Island, Solomon Islands); holotype University Zoological Museum, Copenhagen (not numbered, teste O. S. Tendal, personal communication); paratype MCZ 191379, paratype MCZ 191436 from Tenggano, paratype MCZ from Niupani; all Rennell Island.

Rennellia (section) Clench, 1941, Am. Mus. Novit., (1129): 20 (type species, *Partula cramptoni* Clench 1941, original designation).

renschi Clench, *Eustomopsis* 1958, Natural History of Rennell Island, British Solomon Islands, Copenhagen, Denmark, **2**(27): 198, pl. 19, figs. 9, 10 (Tulagi, Florida Group, Solomon Islands); holotype AMNH 66463, paratype MCZ 92957.

rheophila Bequaert & Clench, *Hydrobia* 1941, Bull. Mus. Comp. Zool., **88:** 8, pl. 2, fig. 4 (estuary of Congo River at Kala-Kala, near Matadi, Belgian Congo); holotype MCZ 112310.

Rhysema (subgenus) Clench & Turner, 1957, Johnsonia, **3:** 236 (type species, *Triton clathratum* Lamarck 1816, original designation).

ricardi Clench & Aguayo, *Cerion* 1951, Rev. Soc. Malacól. "Carlos de la Torre," **8:** 71, pl. 11, fig. 2 (Punta de Tarará, Habana Prov., Cuba); holotype Museo Poey 12669, paratypes MCZ 129421, 129402, 188591.

richardsi Clench, *Hargravesia* 1949, Bull. B. P. Bishop Mus., (196): 47, fig. 27 (N coast of Guadalcanal Island, Solomon Islands); holotype MCZ 161591.

riosi Clench & Turner, *Adelomelon* (*Weaveria*) 1964, Johnsonia, **4:** 162, pls. 83, 101, 102 (about 130 mi. E of Mar del Plata, Argentina, 99 fth.); holotype MCZ 245017.

riveroi Clench, *Geomelania* (*Merrilliana*) 1962, Breviora, (173): 3, pl. 1, fig. 4 (Colonia Ramfis, 20 km W of San Cristobal, República Dominicana); holotype MCZ 230505.

riveroi Turner, *Hemitrochus* 1958, Occas. Pap. Mollusks, **2**(22): 174–177, pl. 24, figs. 5, 6; pl. 27, figs. 1, 2; pl. 29; pl. 30, figs. 3–6 (Cerro Doña Juana, Toro Negro National Forest, Puerto Rico); holotype MCZ 216144.

robertsoni Clench, *Microceramus* (*Spiroceramus*) 1963, Bull. Mus. Comp. Zool., **128:** 406, pl. 3, fig.

1 (Delectable Bay, Settlement, Acklins Island, Bahamas); holotype MCZ 225313.

rocai Clench & Aguayo, *Cerion tridentatum* 1953, Torreira, (18): 2, text fig. 2 (Lagunas Salobres de Boca de Guanabo, Habana, Cuba); holotype Museo Poey 13152, paratypes MCZ 78055, 80729, 129418, 129420.

roseatus Clench, *Drymaeus bahamensis* 1933, Proc. N. Engl. Zool. Club, **13:** 87, pl. 1, figs. 12, 13 (Gt. Inagua Island, Bahamas); holotype MCZ 90104.

rosewateri Clench & Turner, *Calliostoma* (*Kombologion*) 1960, Johnsonia, **4:** 41, pl. 6, fig. 3, pl. 10, fig. 2, pl. 26 (*Oregon* Sta. 1985, 09°45′N, 59°47′W, about 85 mi. SE of Galeota Point, Trinidad, 200 fth.); holotype USNM 612704; paratypes MCZ 235483, 235484.

russelli Clench, *Cerion* 1938, Bull. Mus. Comp. Zool., **80**(14): 528, pl. 1, figs. 5–8 (near Turtle Cove, 4 mi. NNE of The Bight, Central Cat Island, Bahama Islands); holotype MCZ 107534.

russelli Clench, *Chondropoma* 1937, Proc. N. Engl. Zool. Club, **16:** 67, pl. 3, fig. 3 (Gt. Inagua Island, Bahamas); holotype MCZ 90132.

russelli Clench, *Liguus flammellus* 1935, Nautlius, **48**(4): 124, pl. 7, fig. 2 (Mogote Mina Constancia, Viñales, Pinar del Rio, Cuba); holotype MCZ 82980.

russelli Clench, *Microceramus* 1937, Proc. N. Engl. Zool. Club, **16:** 63, pl. 3, figs. 4, 5 (Blue Hole Hill, 2 mi. NNE of Orange Creek, N Cat Island, Bahamas); holotype MCZ 127296.

russelli Clench, *Polydontes* (*Salleana*) 1962, Rev. Mu. Argent. Cienc. Nat. "Bernardino Rivadavia," **8:** 218, pl. 1, fig. 3 (N of La Rucilla [Pico Trujillo], Cordillera Central, Républica Dominicana, 5,800 ft.); holotype MCZ 118212.

salina Clench, *Drymaeus bahamensis* 1959, Bull. Mus. Comp. Zool., **121**(2): 43 (new name for *Drymaeus bahamensis roseatus* Clench 1933, non *Bulimus* [*Drymaeus*] *roseatus* Reeve 1848).

salina Clench, *Physa* 1930, Occas. Pap. Boston Soc. Nat. Hist., **5:** 309, text figs. 1, 2 (Brackish Spring, Skeen's Ranch, Promontory, Box Elder Co., Utah); holotype MCZ 79387, paratypes MCZ 4239.

salina Clench, *Urocoptis bencomoi* 1935, Proc. Boston Soc. Nat. Hist., **41**(1): 4, pl. 2, fig. A ('Saline Madame Doisy', Mahautier, SE end of Gonase Island, Haiti); holotype MCZ 106243.

Salleana (subgenus) Clench, 1962, Rev. Mus. Argent. Cienc Nat. "Bernardino Rivadavia," **8:** 218 (type species, *Polydontes (Salleana) russelli* Clench 1962, original designation).

samana Clench, *Brachypodella* (*Gyraxis*) 1966, Breviora, (245): 11, pl. 2, fig. 5 (Peñon de Maria Luisa, Santa Bartara de Samaná, Républica Dominicana); holotype MCZ 57214.

samana Clench, *Coryda* 1964, Rev. Mus. Argent. Cienc. Nat. "Bernardino Rivadavia," **8:** 225, pl. 1, fig. 1 (Bahía de San Lorenzo, Bahía de Samaná, Prov. de Samaná, Republica Dominicana); holotype MCZ 188240.

samba Cl, *Strombus* 1937, Proc. N. Engl. Zool. Club, **16:** 18, pl. 1, fig. 1 (Wood Cay, West End, Grand Bahamas Island, Bahamas); holotype MCZ 116054.

sana Clench & Archer, *Polygyra* (*Triodopsis*) 1933, Nautilus, **46**(3): 88, pl. 7, figs. 4–6 (34°45′N, 86°31′W, Big Cove, Monte Sano, Huntsville, Madison Co., Alabama); holotype MCZ 95089.

sanagaensis Clench, *Lauistes* (*Lauistes*) 1929, Bull. Mus. Comp. Zool., **69**(6): 120, pl. 1, figs. 7, 8 (Sanaga River, near Sakbayeme, Cameroon); holotype MCZ 78064, paratype MCZ 78065.

sanchezi Clench & Aguayo, *Cerion* 1953, Torreia, (18): 3, figs. 4, 5 (Lengua de Pájaro, Bahía de Lebiza, Mayari, Oriente, Cuba); holotype Mus. Poey 3999, paratypes MCZ 189458.

santomennoi Wetherbee & Clench, *Macroceramus* 1984, Caribb. J. Sci., **20**(1–2): 11, fig. 1, pl. 1, pt. A, left side (1 mi. S of Copey, Monti Cristi Prov., República Dominicana); holotype MCZ 57346 (leftmost figure), paratypes MCZ 57342, 288374.

savaii Clench, *Ostodes* 1949, Bull. B. P. Bishop Mus., (196): 14, figs. 5, 6 (Salailua, Savaii Island, Samoan Islands); holotype Bishop Museum 9710, paratypes MCZ 140501.

schepmani Turner, *Oocorys* 1948, Johnsonia, **2**(26): 190 (new name for *O. elongata* Schepman 1909, non Locard 1897).

schevilli Clench & Archer, *Thersites* 1938, J. Conch., **21:** 23, pl. 1, fig. 1 (foot of Mt. Walker, S of Hughenden, Queensland); holotype MCZ 99055, paratypes Queensland Museum, South Brisbane, Queensland (QMMO) 1968.

schoutedeni Bequaert & Cl, *Lobogenes* 1936, Mem. Mus. R. Hist. Nat. Belg., 2nd ser., (3): 164, pl. 1, figs. 1, 2 (Ango-Ango, 4 km S of Matadi, Congo River, Belgian Congo); holotype MCZ 59805.

schroederi Clench & Aguayo, *Calliostoma* (*Calliostoma*) 1938, Mem. Soc. Cubana Hist. Nat., **12:** 377, pl. 28, fig. 3 (*Atlantis* Sta. 2981, 22°48′N, 78°48′W, off northern Cuba, 225 fth.); holotype MCZ 135002.

schwabi Clench, *Egeria* 1929, Bull. Mus. Comp. Zool., **69:** 122, pl. 1, figs. 1, 2 (Lobetal, Lower Sanaga River, Cameroon); holotype MCZ 78072.

scotti Clench, *Plagioptycha* 1963, Bull. Mus. Comp. Zool., **128**(8): 411, pl. 3, fig. 3 (2 mi. S of Binnacle Hill Settlement, Acklins Island, Bahamas); holotype MCZ 225311.

Septariellina (genus) Bequaert & Clench, 1936, Mem. Mus. R. Hist. Nat. Belg., 2nd ser., (3): 163, fig. 1 (type species, *Septariellina congolensis* Bequaert & Clench 1936, original designation).

Setaepoma (genus) Clench, 1955, Nautilus, **68**(4): 134 (type species, *Japonia hedigeri* I. and B. Rensch 1936, original designation).

shattucki Bequaert & Clench, *Drymaeus* 1931, Occas. Pap. Boston Soc. Nat. Hist., **5:** 424 (Chichen Itza, Yucatan); holotype MCZ 79396, paratypes MCZ 79409.

shrevei Clench & Aguayo, *Cerion* (*Umbonis*) 1952, Occas. Pap. Mollusks, **1**(17): 436, pl. 57, fig. 4 (near North West Point, Little Inagua Island, Bahama Islands); holotype MCZ 192287.

sisal Clench & Aguayo, *Cerion* (*Umbonis*) 1952, Occas. Pap. Mollusks, **1**(17): 427, pl. 57, fig. 3 (E. side, Boca de Mosquito, Mariel, Pinar del Rio, Cuba); holotype MCZ 181992.

soluta Clench & Turner, *Taheitia* 1948, Occas. Pap. Mollusks, **1**(13): 190, pl. 23, fig. 4; pl. 24, figs. 5, 6 (Bavatu, Varna Mbalavu, Lau Group, Fiji Islands); holotype Bishop Museum 179895, paratypes MCZ 157754.

spelunca Turner & Clench, *Physa* 1974, Nautilus, **88:** 82, figs. 1–19 (cave stream, about 800–900 ft. from the entrance, in Lower Kane Cave, near Kane, about 12 mi. E of Lovell, E side of the Big Horn River, Big Horn Co., Wyoming, 3,000 ft.); holotype MCZ 280016.

spinella Clench, *Cassis madagascariensis* 1944, Johnsonia, **1**(16): 15, pl. 8 (Tortugas, Florida); holotype MCZ 140761.

springeri Clench & Turner, *Calliostoma* 1960, Johnsonia, **4:** 71, pl. 52, figs. 1, 2 (*Oregon* Sta. 1283, 29°6′N, 88°19′W, about 38 mi. E of Southeast Pass, Mississippi Delta, Louisiana, 260 fth.); holotype USNM 612703.

stevensoni Clench, *Foxidonta* 1950, Rev. Soc. Malacól. "Carlos de la Torre," **7**(2): 59, text figs. 1–3 (Fiu, Northern Malaita Island, Solomon Islands); holotype MCZ 186268.

strongi Bequaert & Clench, *Afroditropis* 1936, Rev. Zool. Bot. Afr., **29:** 103, pl. 2, figs. 8, 9 (Makato, French Congo, on the right bank of the Congo Rivers, between Lukolcla and Irebu); holotype MCZ 77196.

subflava Clench, *Physa fontinalis* 1926, J. Conch., **18:** 12 (new name for *Physfontinalis inflata* Moquin-Tandon 1855, non *Physa inflata* Lea 1841 and *Physa inflata* Adams & Angus 1864).

Surinamia (subgenus) Clench, 1933, Nautilus, **47:** 71 (type species, *Asolene* [*Surinamia*] *fairchildi* Clench 1933, original designation).

tablasensis Clench & Archer, *Helicina ignava* 1931, Occas. Pap. Boston Soc. Nat. Hist., **5:** 339 (Agcalatac, Tablas Island, Philippines); holotype MCZ 47235, paratype MCZ 21536 (only specimens mentioned).

Tamu (genus) Gustafson, Turner, Lutz, Vrijenhoek, 1998, Malacologia, **40**(1–2): 90 (type species *Tamu fisheri* Gustafson, Turner, Lutz & Vrijenhoek, 1998, original designation).

Tectininus (subgenus) Clench & Abbott, 1942, Johnsonia, **1**(4): 4 (type species, *Echininus* [*Tectininus*] *nodulosus* Pfeiffer 1834, original designation).

tejedori Clench & Aguayo, *Chondropoma* (*Parachondrodes*) 1946, Rev. Soc. Malacól. "Carlos de la Torre," **4**(2): 52–53, text figure (El Ocujal, Mayarí, Oriente, Cuba); holotype Museo Poey 3997, paratype MCZ 178197.

Thaanumella (genus) Clench, 1946, Occas. Pap. B. P. Bishop Mus., **18**(13): 201 (type species, *Diadema carolinarum* Möllendorff 1897, original designation).

Thaanumellinae (family) Clench, 1946, Occas. Pap. B. P. Bishop Mus., **18**(13): 199 (type genus, *Thaanumella* Clench 1946).

thaanumi Clench & Turner, *Truncatella* (*Truncatella*) 1948, Occas. Pap. Mollusks, **1**(13): 165, pl. 25, fig. 6 (Ulali Island, Truk Group, Caroline Islands); holotype MCZ 159379.

Thaisella (subgenus) Clench, 1947, Johnsonia, **2**(23): 69 (type species, *Purpura trinitatensis* Guppy 1869, original designation).

thermalis Bequaert & Clench, *Achatina* (*Pintoa*) 1936, Bull. Mus. R. Hist. Nat. Belg., **12**(32): 1, figs. 1–10 (Katana, W shore of Lake Kiva, near hot mineral springs of Kakonds, Belgian Congo); holotype Institut Royal des Sciences naturelles de Belgique, Bruxelles, Type no. 173, inventoried under I. G. 10.010; paratypes MRAC 201309, 201310; paratypes MCZ 111711.

thielei Bequaert & Clench, *Callistoplepa* 1934, Rev. Zool. Bot. Afr., **26:** 115, pl. 2, figs. 8–10 (Utengule near Langenburg, Tanganyika Territory, Africa); holotype ZMB 53177a, fig. 8, paratypes ZMB 53177b (Kilias, 1992:179) (2), paratypes MCZ 98686.

Thomeomaizenia (subgenus) Bequaert & Clench, 1936, Rev. Zool. Bot. Afr., **29**(1): 99 (type species, *Cyclophorus vandellii* Nobre 1886, monotypy).

tiburonense Clench & Turner *Epitonium* 1952, Johnsonia, **2:** 305, pl. 143 (Aquin Dept. du Sud, Haiti); holotype USNM 440128, paratype MCZ 187959.

tiburonica Clench, *Archegocoptis* 1935, Proc. Boston Soc. Nat. Hist., **41:** 6, pl. 1, fig. I (above Tardieu, Mt. La Hotte, Haiti, 3–4,000 ft.); holotype MCZ 108591.

tipperi Turner, *Xylophaga* 2002, Bull. Mus. Comp. Zool. **157**(4): 259, pl. 29 (26°04′N, 80°04′W, about 3.2 mi. off Fort Lauderdale, Florida, 152.4 m); holotype MCZ 316736, paratype MCZ 316737.

togöensis Bequaert & Clench, *Achatina* 1934, Rev. Zool. Bot. Afr., **26:** 112, pl. 1, figs. 1–4 (Bismarckburg, Togo, Africa); holotype ZMB 47176a, fig. 2, paratypes ZMB 4717b; (Kilias 1992:179) (2), paratypes MCZ 98688.

Tomlinella (subgenus) Clench & Turner, 1948, Johnsonia, **2:** 159 (type species, *Truncatella scalaris* Michaud 1830, original designation).

Tomlinitella Clench & Turner, 1948, Occas. Pap. Mollusks, **1**(13): 169 (new name for *Tomlinella* Cl & Turner 1948, non *Tomlinella* Viader 1938).

tongana Clench & Turner, *Taheitia* 1948, Occas. Pap. Mollusks, **1**(13): 190, pl. 23, fig. 6 (0.5 mi. from Vaigana, Eua Island, Tonga Islands); holotype Bishop Museum 87703, paratypes MCZ 157757.

torrei Clench & Aguayo, *Calliostoma* (*Calliostoma*) 1940, Mem. Soc. Cubana Hist. Nat., **14**(1): 79, pl. 14, fig. 5 (*Atlantis* Sta. 3985, 23°13′N, 81°22′W, off

Matánzas, Matánzas Prov., Cuba, 385 fth.); holotype MCZ 135165.

torrei Clench & Aguayo, *Cepolis* (*Jeanneretia*) 1933, Nautilus, **47:** 22, pl. 3, figs. 7, 8 (cave in the Sierra Hato Nuevo, near Marti, Matánzas Prov., Cuba); holotype MCZ 59730.

torrei Clench, *Liguus fasciatus* 1934, Occas. Pap. Boston Soc. Nat. Hist., **8:** 114, pl. 6, figs. 5, 6 (Punta del Este, Isle of Pines, Cuba); holotype MCZ 58805.

trachydermon Clench & Archer, *Thersites* 1938, J. Conch., **21:** 21, pl. 1, fig. 5 (24 mi. NW of Cardwell, Queensland); holotype MCZ 73284.

trochiformis Clench, *Goodrichia* 1929, Bull. Mus. Comp. Zool., **69**(6): 118, pl. 1, figs. 3, 4 (Man River, near Sakbayeme, Cameroon); holotype MCZ 78066, paratypes MCZ 78067, 78068, 78071.

trujilloi Clench, *Oliva* 1938, Nautilus, **51**(4): 111, pl. 9, figs. 3–5 (Puerto Plata, Santo Domingo, 5 fth.); holotype MCZ 57240.

tuftsensis Turner, *Chlamys* (*Zygochlamys*) 1967, N. Z. J. Geol. Geophys., **10**(2): 446–455, figs. 1–5 (approx. 77°31′S, 162°E, outwash gravel, Bull Pass, Wright Valley, McMurdo Sound, Antarctica, 1,000 ft. (305 m elev. [from early to middle Pleistocene]); holotype MCZ 256085, paratype MCZ 256086.

tumidula Clench & Aguayo, *Eutrochatella* (*Microviana*) 1957 [in] Aguayo, C. G., and M. L. Jaume, Mem. Soc. Cubana Hist. Nat. "Felipe Poey," **23:** 119, pl. 1, fig. 6 (Cerro de los Portales, Camayén, Barrio de Bariay, Gibara, Oriente, Cuba); holotype Museo Poey 13260, paratypes MCZ 212978.

turbinella Clench & Archer, *Polygyra* (*Stenotrema*) 1933, Nautilus, **46**(3): 89, pl. 7, figs. 1–3 (34°39′N, 86°15′W, 2–4 mi. E of Woodville, Jackson Co., Alabama); holotype MCZ 95140.

turgidus Clench & Aguayo, *Caracolus sagemon* 1951, Mem. Soc. Cubana Hist. Nat., **20:** 67, pl. 42, figs. 1–3 (Mina Caledonia, Mayarí, Oriente, Cuba); holotype Museo Poey 17205, paratype MCZ 187544.

turnerae Clench & Aguayo, *Cerion* (*Umbonis*) 1952, Occas. Pap. Mollusks, **1**(17): 423, pl. 53, figs. 4–7 (Lydia Point, Gt. Inagua Island, Bahama Islands); holotype MCZ 184623.

turnerae Clench, *Chondropoma* 1951, J. Conchy., **90:** 271, fig. 1 (Mona Island, Puerto Rico); holotype MCZ 171039.

ultima Clench & Archer, *Helicostyla cincinniformis* 1931, Occas. Pap. Boston Soc. Nat. Hist., **5:** 335, pl. 17, fig. 4 (Lubang Island, Philippines); holotype MCZ 79169, paratypes MCZ 79170.

ulugurensis Bequaert & Clench, *Edentulina* 1936, J. Conch., **20:** 213, text figs. 11, 12 (Vituri, Ulugura Mts., Tanganyika Territory, Africa, 2,500 ft.); holotype MCZ 59926.

unidentatus Clench, *Nesonanina* 1957, Am. Mus. Novit., (1863): 4, figs. 5, 7 (Rambutyo Island, Admiralty Islands); holotype AMNH 73488, paratypes MCZ 188138.

Urocoptola (section) Clench, 1935, Proc. Boston Soc. Nat. Hist., **41**(1): 3 (type species, *Cylindrella gruneri* Dunker 1844, original designation).

usambarensis Bequaert & Clench, *Edentulina* 1936, J. Conch., **20:** 115, text fig. 13 (Lutindi, Usambara Mts., Tanganyika Territory, Africa, 4,000 ft.); holotype MCZ 59919.

utahensis Clench, *Physa lordi* 1925, Occas. Pap. Mus. Zool., Univ. Mich., (161): 8, pl. 1, fig. 5 (Utah Lake, 2 mi. S of Lehi, Utah); holotype UMMZ Walker collection 4257. The Walker number on the UMNZ lot does not correspond to this species. It is a *Clausilia* from France (teste Graf, personal communication). Since the holotype could not be located, the other type lots are regarded as syntypes, UMMZ 229549, MCZ 36541, 30982.

utowana Clench, *Cerion* (*Strophiops*) 1933, Proc. N. Engl. Zool. Club, **13:** 92, pl. 1, figs. 1, 2 (East Plana Key, Bahamas); holotype MCZ 101157.

utowana Clench, *Plagioptycha macrodon* 1952, Rev. Soc. Malacól. "Carlos de la Torre," **8:** 114, pl. 15, figs. 4–6 (Bannermantown, Eleuthera Island, Bahamas); holotype MCZ 103111, paratypes MCZ 103111 (*P. duclusiana utowana* Clench on labels).

utowana Clench, *Succinea* 1933, Proc. N. Engl. Zool. Club, **13:** 85, pl. 1, figs. 18, 19 (near Victoria Hill Settlement, Watling Island, Bahamas); holotype MCZ 101171.

utowanae Clench, *Brachypodella* 1932, Proc. N. Engl. Zool. Club, **12:** 104 (Beata Island, Santo Domingo); holotype MCZ 81492.

Valvatorbis (genus) Bequaert & Clench, 1936, Mem. Mus. R. Hist. Nat. Belg., 2nd ser., (3): 166 (type species, *Valvatorbis mauritii* Bequaert & Clench 1936, original designation).

vanattai Clench & Aguayo, *Cerion* 1951, Rev. Soc. Malacól "Carlos de la Torre," **8:** 78, pl. 11, fig. 12 (Playa Larga, Boca de Janco, Baracoa, Oriente, Cuba); holotype Museo Poey 12671, paratypes MCZ 66713, 128950, 188592.

vanattai Clench, *Spiroceramus* (*Spiroceramus*) 1967, Breviora, Mus. Comp. Zool., (260): 5, pl. 1, fig. 4 (Los Cangilones, Sierra de Cubitas, Camagüey Prov., Cuba); holotype MCZ 256083, paratypes MCZ 131387, 131391, 188844.

vanderrieti Clench, *Kalendyma* 1966, Nautilus, **80:** 52, pl. 3, figs. 1, 2 (Ata'a, Malaita, Solomon Islands); holotype MCZ 260885.

vanderrieti Clench, *Trochomorpha* 1965, Breviora, (224): 3, pl. 2, figs. 1, 2 (Ata'a, Malaita Island, Solomon Islands); holotype MCZ 251176, paratypes MCZ 251177, 247959.

vanhyningi Clench & Smith, *Dinocardium robustum* 1944, Johnsonia, **1**(13): 11, pl. 7 (Sanibel Island, Florida); holotype MCZ 151146.

vegai Clench & Turner, *Lyria* (*Lyria*) 1967, Nautilus, **80**(3): 83–84, fig. 1 (fish trap, Cabo Rojo, Prov. Pedernales, Républica Dominicana, Hispaniola); holotype MCZ 256494.

verae 'Clench' Branham, *Natica canrena* 1954, Shells Along the Florida Shore, St. Petersburg, p. 26, fig.

251 (Marco Island, Florida [error for *Naticarius verae* Rehder 1947]).

Verdichloritis (subgenus) Clench, 1957, Breviora, (76): 1 (type species, *Eastomopsis* [*Verdichloritis*] *polingi* Clench 1957, original designation).

vigoensis Clench & Archer, *Chloraea thersites* 1933, Pap. Mich Acad. Sci. Arts Lett., **17:** 537, pl. 57, figs. 4, 5 (Monte Vigo, Lubang, Philippines); holotype MCZ 81384.

viridis Clench, *Liguus fasciatus* 1934, Occas. Pap. Boston Soc. Nat. Hist., **8:** 105, pl. 6, fig. 11 (La Caoba, near Dolores, Central Soledad, Cienfuegos, Santa Clara, Cuba); holotype MCZ 59507.

voluminosa Clench & Banks, *Polygyra* (*Strenotrema*) 1932, Nautilus, **46:** 16, pl. 2, figs. 6, 7 (35°38′N, 83°39′W, Blowing Springs, Cliff Ridge, Nantahala Gorge, Swain Co., North Carolina); holotype MCZ 82530.

Wahgia (genus) Clench & Turner, 1959, J. Malacol. Soc. Aust., (3): 4 (type species *Wahgia juliae* Clench & Turner 1959, original designation).

walkeri Clench, *Liguus fasciatus* 1933, Nautilus, **46:** 91, pl. 7, figs. 7–9 (Hammock 9, Pinecrest Region, Central Everglades, Florida); holotype MCZ 79299.

wallisi Clench & Cooke, *Succinea* 1945, Occas. Pap. B. P. Bishop Mus., **18**(8): 133, fig. 1 (Papenoo Valley, Tahiti, Niu (Greater Tahiti), Society Islands, at 50–500 ft.); holotype Bishop Museum 87027, paratype MCZ 146394.

wansoni Bequaert & Clench, *Potadoma* 1941, Bull. Mus. Comp. Zool., **88:** 9, pl. 1, fig. 9, 11, 12 (estuary of the Congo River, Matadi, Belgian Congo); holotype MCZ 112268.

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Publications of Ruth D. Turner

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Comments and New Records for the American Genera *Gea* and *Argiope* with the Description of New Species (Araneae: Araneidae)

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COMMENTS AND NEW RECORDS FOR THE AMERICAN GENERA *GEA* AND *ARGIOPE* WITH THE DESCRIPTION OF A NEW SPECIES (ARANEAE: ARANEIDAE)

HERBERT W. LEVI[1]

ABSTRACT. There are one species of *Gea* and seven species of *Argiope* in the Americas. Distributions of *Gea* and *Argiope* species are recorded with new records from South America. Only one new species, *A. ericae,* from southern Brazil to northern Argentina, was found and is here described. The coloration of the female abdomen of *Argiope* species differs more than the visible differences of the genitalia. Males are separated by differences in palpi, the attachment of the embolus to stipes, and the shape of the coiled embolus.

INTRODUCTION

In 1968, I started my araneid revisions with the genera *Gea* and *Argiope.* These genera were first because they are the most distinct of the araneid genera, separated from most others by the presence of a procurved posterior eye row. At the time, I had mostly North American collections from the MCZ and AMNH. The individual variation among specimens was astonishing, especially in the structure of the epigynum (these are not again illustrated here). At the time, Willis Gertsch (personal communication) stressed that species could not be variable; when differences were found, they must indicate two species. I disagreed because when many specimens were examined, there were intermediates. These were the taxonomic issues of arachnologists in the 1960s.

This is an update of the 1968 revision. Since 1968, many additional South American specimens have become available, begging to be examined, especially in view of today's better understanding of variation. When I started this revision I expected several species to be new, but I found only one. In the 1960s lack of funds limited the amount of data that could be included in the paper, so the localities of specimens were omitted, represented only by dots on a map. Although lengthy, both new localities and disposition of specimens are provided here, much abbreviated for common species, except for southern border specimens. I have not repeated information published in 1968, except that essential for maps and diagnoses.

At present, I have revised most American araneid genera and have examined the *Argiope* of the Pacific area (Levi, 1983). The Chinese *Argiope* have been illustrated by Yin (1997), the African species by Bjørn (1997), and the Mideastern species by Levy (1998).

METHODS

The methods used here were the same as in the revisions of other American araneid genera (Levi, 1993).

Specimens came from the following collections:

AMNH	American Museum of Natural History, New York, United States; N. Platnick, L. Sorkin
BMNH	Natural History Museum, London, England; J. Beccaloni
CAS	California Academy of Sciences, San Francisco, California,

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	United States; C. Griswold, D. Ubick
FSCA	Florida State Collection of Arthropods, Gainesville, Florida, United States; G. B. Edwards
IBSP	Instituto Butantan, São Paulo, Brazil; A. Brescovit
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; L. Baert
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; C. L. Scioscia
MCN	Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil; E. H. Buckup, M. A. L. Marques
MCP	Museu de Ciências, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil; A. A. Lise
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts, United States
MHNMC	Museo de Historia Natural, Medellín, Colombia; L. A. Zamudio
MLP	Museo de La Plata, La Plata, Argentina; C. Ituarte, L. A. Pereira
MZSP	Museu de Zoologia, Universidade de São Paulo, São Paulo, SP, Brazil; R. Pinto da Rocha
SMNK	Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany; H. Höfer
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C., United States; J. Coddington, S. F. Larcher
ZMUC	Zoologisk Museum, Copenhagen, Denmark; N. Scharff

RESULTS

Species Characters. The eye arrangement, procurved posterior eye row, and structure of the male palpus place *Gea* close to *Argiope.*

Females of *Argiope* are easiest to determine by their coloration as epigyna of many are quite similar (Levi, 1968). This differs from Bjørn's (1997) observations of African *Argiope,* which show much greater differences in genitalia as well as coloration. Extracting the broken male embolus tip stuck in the copulatory ducts inside of the epigynum is helpful for determining females in faded specimens.

Males of *Argiope* can be separated by examining the palpus. The palpi of most species are much alike, differing, however, in the attachment of the embolus to the stipes (arrow, Fig. 25) and the shape and structure of the curved embolus.

The relatively small differences between *Argiope* species in morphology of the genitalia and the consistent differences in coloration of the abdomen reminds one of similar differences in the theridiid widow spiders, *Latrodectus* (Abalos, 1980). Both genera also have a long, thread-shaped embolus that breaks off and plugs the epigynum. In both genera, relatively common species have been overlooked in well-collected areas.

Gea heptagon is probably introduced from the South Pacific where it and other species of *Gea* are found. There are seven species of *Argiope* in the Americas, one in Europe, 13 in Africa and Madagascar, and about 29 in China. Only one, *A. trifasciata,* is cosmopolitan. The similarity of genitalia suggests all but *A. aurantia* are close to *A. trifasciata.*

TAXONOMIC SECTION

Gea C. L. Koch

Gea C. L. Koch, 1843: 101. Type species *Gea spinipes* C. L. Koch, 1843: 101, pl. 823, from the East Indies.

Diagnosis. Gea species, together with those of *Argiope,* differ from most araneid genera by having the posterior eye row strongly procurved, from *Mangora* by the low thoracic region of the carapace and by

lacking trichobothria on the third tibia, and from *Mecynogea* by the wider carapace and different structure of the palpus.

Gea specimens are smaller than *Argiope* and have larger posterior median eyes. In females of *Gea*, the eyes of the posterior eye row are almost equally spaced (Fig. 5), whereas in *Argiope*, the median eyes are closer to each other than to the laterals.

Gea heptagon (Hentz)
Maps 1A; Figures 1–8

Epeira heptagon Hentz, 1850: 20. Type specimens destroyed, from North Carolina and Alabama.
Gea heptagon:—Keyserling, 1892: 76, pl. 3, fig. 58. Levi, 1968: 324, figs. 1–24, ♀♂. Platnick, 2003.

Diagnosis. The small size of females, the shape of the abdomen (Figs. 4, 5), the epigynum with a ventral transverse slit and paired posterior openings (Figs. 1–3), and the male palpus with the embolus only gently curved, held by a large conductor (Fig. 8), distinguish the species from others. Differences of the first tibia are unreliable.

Variation. Total length of females 3.7–6.4 mm, males 2.6–4.1 mm. The color of the abdomen is variable. There may be transverse lines or a dark folium. The illustrations of a female (Figs. 1–5) were made from a specimen from Florida, male (Figs. 6–8) from a specimen from Honduras.

Natural History. Found in soybean field in Arkansas, in high grass in Florida. The female drops from the web when disturbed.

Distribution. Pacific, probably introduced to America and found from eastern United States and West Indies (Map 1A), probably to Argentina.

Additional Records. UNITED STATES, NORTH CAROLINA *Dare Co.*: Kill Devil Hills, 12 Sep. 1956, 1♀ (K. V. Krombein, USNM). GEORGIA *Bullock Co.*: Statesboro, 1984, ♀ (E. Dismer, USNM). *Chatham Co.*: Rt. 95, nr. South Carolina border, 1 Aug. 1985, ♀♂ (J. Coddington, USNM). ALABAMA *Dallas Co.*: Selma, ♀ (USNM). FLORIDA *Franklin Co.*: St. Teresa, 23 Mar. 1961, ♀ (J. Carico, USNM). *St. Lucie Co.*: Fort Pierce, ♀♂ (M. Mikkelson, USNM); 7 Sep. 1985, ♀ (P. Mikkelson, USNM). ARKANSAS *Chicot Co.*: 29 Aug. 1962, ♀ (CAS). *Mississippi Co*: Big Lake, 23 June 1966, ♂ (W. Peck, CAS). LOUISIANA *Cameron Par.*: Cameron, ♀ (USNM). OKLAHOMA *Garfield Co.*: Enid, 36°24′N, 97°54′W, 28 July 1989, ♀ (L. E. Anhorn, USNM). CALIFORNIA *San Diego Co.*: Del Mar, ♀ (M. Martinez, USNM); Los Angeles, ♀♂ (USNM). MEXICO *San Luis Potosí*: Huichihuayan, 98°50′N, 21°19′W, 24 July 1966, ♂ (J., W. Ivie, AMNH). HONDURAS *Atlantida*: Lancetilla, 20 July 1929, ♂ (A. M. Chickering, MCZ). *Copan*: Copan, 16 Feb. 1937, ♂ (MCZ). COSTA RICA Turrialba, 25–31 May l962, ♀ (H. Ruckes, AMNH). PANAMA Balboa, 1 Aug. 1943, ♂ (J. B. Duncan, AMNH).

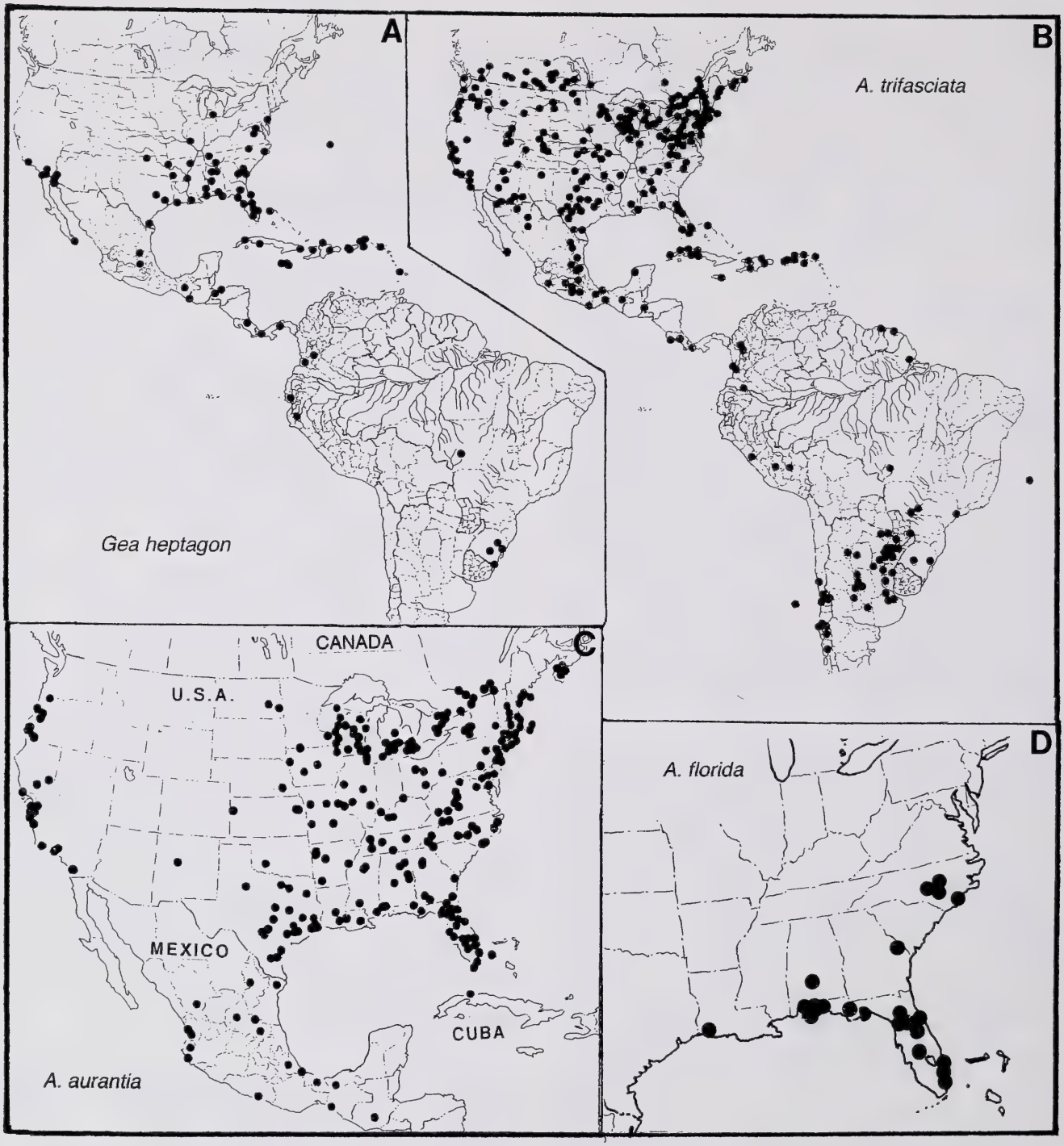
BAHAMA ISLANDS Grand Bahama Island, 13 May 1953, ♀ (L. Giovannoli, AMNH). DOMINICAN REPUBLIC Ciudad Trujillo [Santo Domingo], nest of *Sceliphron* wasp, 1947, ♀♂ (H. F. Allard, USNM). PUERTO RICO SW Guayama, Pta. Pozuela, 25 Dec. 1985, ♀ (V., B. Roth, CAS); Aguas Bueno, 5 Nov. 1971, imm. (J. Carico, USNM). VIRGIN ISLANDS St.Croix, 1–11 Sep. 1966, ♀ (A. M. Chickering, USNM).

COLOMBIA *Valle*: nr. Cali, 1,000 m elev., 1977, ♂ (W. Eberhard, MCZ); Palmira, 27 June l964, ♂ (R. Hunter, CAS). ECUADOR Guayaquil, 22 Mar. 1942, ♂ (Landes, CAS). PERU *Piura*: Hiquéron, July 1941, ♂ (H. E., D. L. Frizzell, CAS). BRAZIL *Mato Grosso*: S. Antônio de Levergera, 8 Sep. 1992, ♀ (M. E. Marques, MCP 2558). *Rio Grande do Sul*: Guaíba, 1 Jan. 1989, ♀♂ (A. B. Bonaldo, MCN 18009); 24–27 Dec. 1992, ♀♂ (A. B. Bonaldo, MCN 22643); Montenegro, 7 July 1977, ♀ (H. A. Gastal, MCN 6177); Porto Alegre, 21 Sep. 1992, ♂ (A. Bonaldo, MCP 2051); Taim, Rio Grande, 18 Mar. 1982, ♂ (J. Grazia, MCN 10247); Vila Nova, 23 May 1991, ♀ (F. Garcia, MCP 2729); Xangrila, 5 Jan. 1993, 24 Feb. 1993, ♀ (A. A. Lise, MCP 2902, 2974). ARGENTINA Specimens have been examined from northern Argentina without recording the data.

Argiope Audouin

Argyope Audouin, 1826: 121. Type species designated by Thorell, 1869: 51, *Argiope lobata* from the Mediterranean and Africa.
Argiope Audouin,1827: 328.
Miranda C. L. Koch 1835: 128, pl. 14. Type species *Miranda transalpina* C. L. Koch (=*Argiope bruennichi* (Scopoli)). First synonymized by Thorell, 1869: 51.
Metargiope F. P.-Cambridge, 1903: 451. Type species by monotypy *Argiope trifasciata.*

Note. The International Commission on Zoological Nomenclature (Opinion 1038, 1975: 105) validated the name *Argiope* Audouin, 1826, and placed it on the Official List of Generic Names in Zoology with the



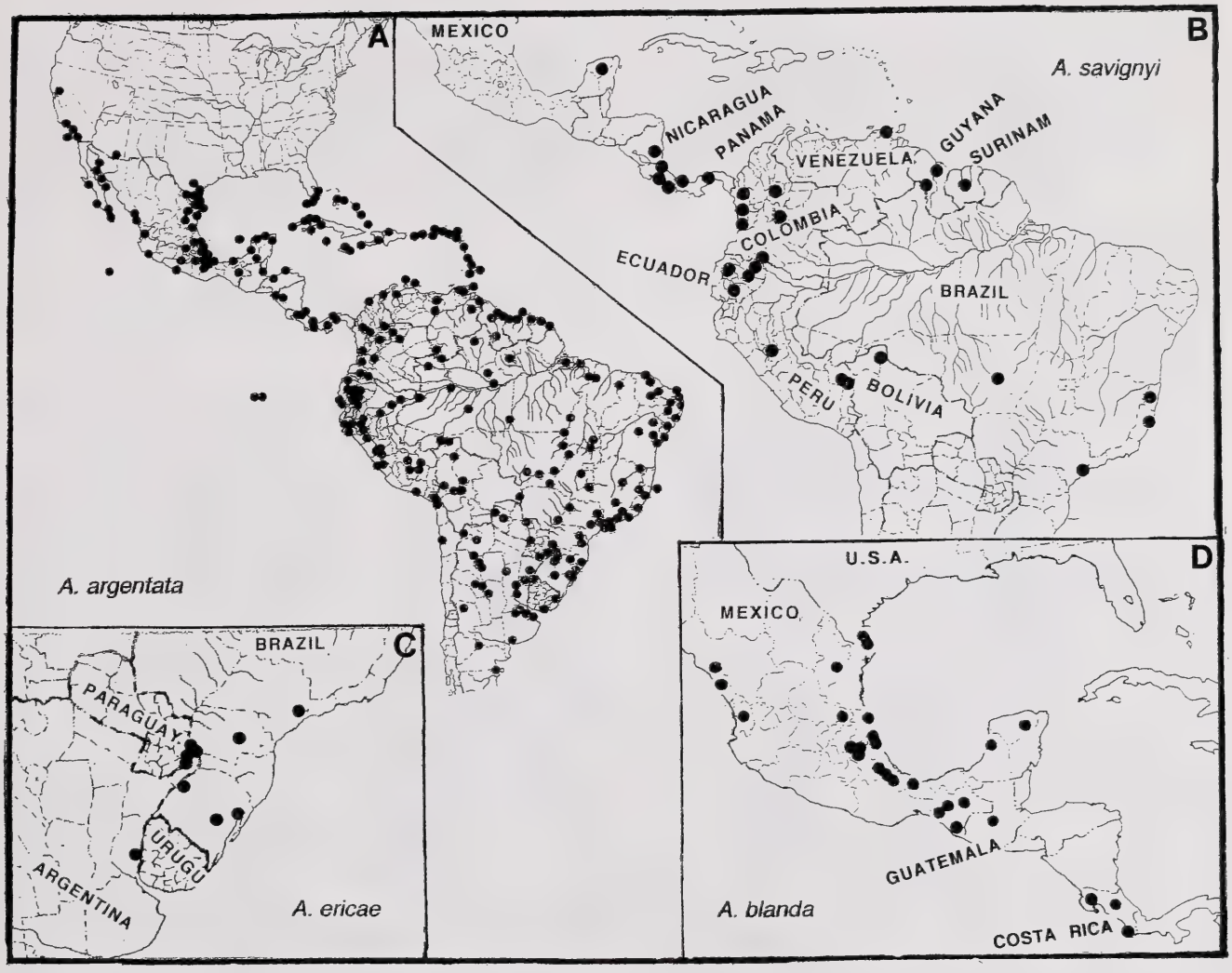
Map 1. Distribution of *Gea* and *Argiope* species.

number 2009, and considered *Argyope* an incorrect spelling.

Diagnosis. Argiope and *Gea* differ from most araneids by having the posterior eye row procurved (Figs. 12, 14), from *Mangora* by their low thoracic region of the carapace and by lacking trichobothria on the third tibia, and from *Mecynogea* by a wider carapace and a different structure of the palpus.

Argiope differs from *Gea* (Figs. 5, 7) by having the posterior median eyes smaller and closer to each other than to the laterals (Figs. 12, 14) and by females being larger (Fig. 12) than those of *Gea*.

Unlike most araneids, the epigynum of



Map 2. Distribution of *Argiope* species.

Argiope lacks a scape; it usually has a bulging hood with a cavity (Figs. 9, 10) or cavities below (Figs. 18, 20). The male palpus has a separate sclerite, the stipes, between the radix and embolus (Figs. 16I, 17I). The palpus lacks a terminal apophysis and has an elaborate conductor (Figs. 16C, 17C) supporting the embolus (Figs. 16E, 17E). A thin curved branch extends from the median apophysis (Figs. 16M, 17M).

Key to Females

1 Venter of abdomen with a central transverse white band (Figs. 39, 49) that may be broken (Fig. 58) 5
– Venter of abdomen without central transverse band (Figs. 11, 21, 30) or lines (Fig. 67) on black 2
2(1) Dorsum of abdomen with median black band (Fig. 12); epigynum a longitudinal bar (Figs. 9, 10); North America, Mexico (Map 1C) ..... *aurantia*
– Abdomen otherwise 3
3(2) Dorsum of abdomen with transverse lines or bands (Figs. 22, 68) 4
– Dorsum of abdomen with pair of posterior, longitudinal bands (Fig. 31); SE United States (Map 1D) ..... *florida*
4(3) Dorsum of abdomen with transverse bands (Fig. 68), abdomen with pair of anterior tubercles and three lateral pairs of tubercles (Fig. 68); São Paulo State to NE Argentina (Map 2C) ..... *ericae*
– Dorsum of abdomen with transverse lines (Fig. 22); cosmopolitan (Map 1B) ..... *trifasciata*
5(1) Transverse, ventral band wider than length of anterior median black trapezoid (Fig. 49); Texas to Central America (Map 2D) ..... *blanda*
– Transverse band narrower than length of black patch (Figs. 39, 58) 6
6(5) Transverse band pointing anteriorly and broken in middle (Fig. 58); dorsum with posterior black (Fig. 59); epigynum enlarged posteriorly (Fig. 55, 56); Mexico to Argentina (Map 2B) .....

..... *savignyi*

– Transverse band straight, rarely broken (Fig. 39); dorsum with posterior having windows in black area (Fig. 40); epigynum smaller posteriorly (Figs. 36, 37); Florida, Texas, California to southern Brazil (Map 2A) ..... *argentata*

KEY TO MALES

1 Embolus straight (Fig. 15); North America, Mexico (Map 1C) ..... *aurantia*
– Embolus and conductor coiled (Figs. 16, 17, 26, 44) 2
2(1) Base of sclerotized embolus with jointed to large flat stipes (arrow, Figs. 25, 34) 3
– Base of embolus turning into a screw-shaped base (Figs. 43, 53, 62), stipes small, partly hidden (I in Figs. 16, 17) 4
3(2) Curl of embolus small, showing stipes and tegulum on each side (Fig. 26); cosmopolitan (Map 1B) ..... *trifasciata*
– Curl of embolus large, hiding stipes and tegulum (Fig. 35); SE United States (Map 1D) ..... *florida*
4(2) Venter of abdomen with a pair of white patches on black (Fig. 70); São Paulo State to NE Argentina (Map 2C) ..... *ericae*
– Venter usually with broken longitudinal lines (Figs. 41, 51, 60) 5
5(4) Tip of embolus with a spur (arrow, Fig. 43; Figs. 44, 45); Florida, Texas, California to Argentina (Map 2A) ..... *argentata*
– Embolus tip without spur (Figs. 54, 63) 6
6(5) Embolus coil with a basal cone (arrow, Fig. 53; Fig. 54); Texas to Central America (Map 2D) ..... *blanda*
– Embolus without cone (Figs. 62, 63); Mexico to southern Brazil (Map 2B) ..... *savignyi*

Argiope aurantia Lucas
Map 1C; Figures 9–15

Argyope aurantia Lucas, 1833: 86, pl. 5, fig. 1. Female holotype from North America.

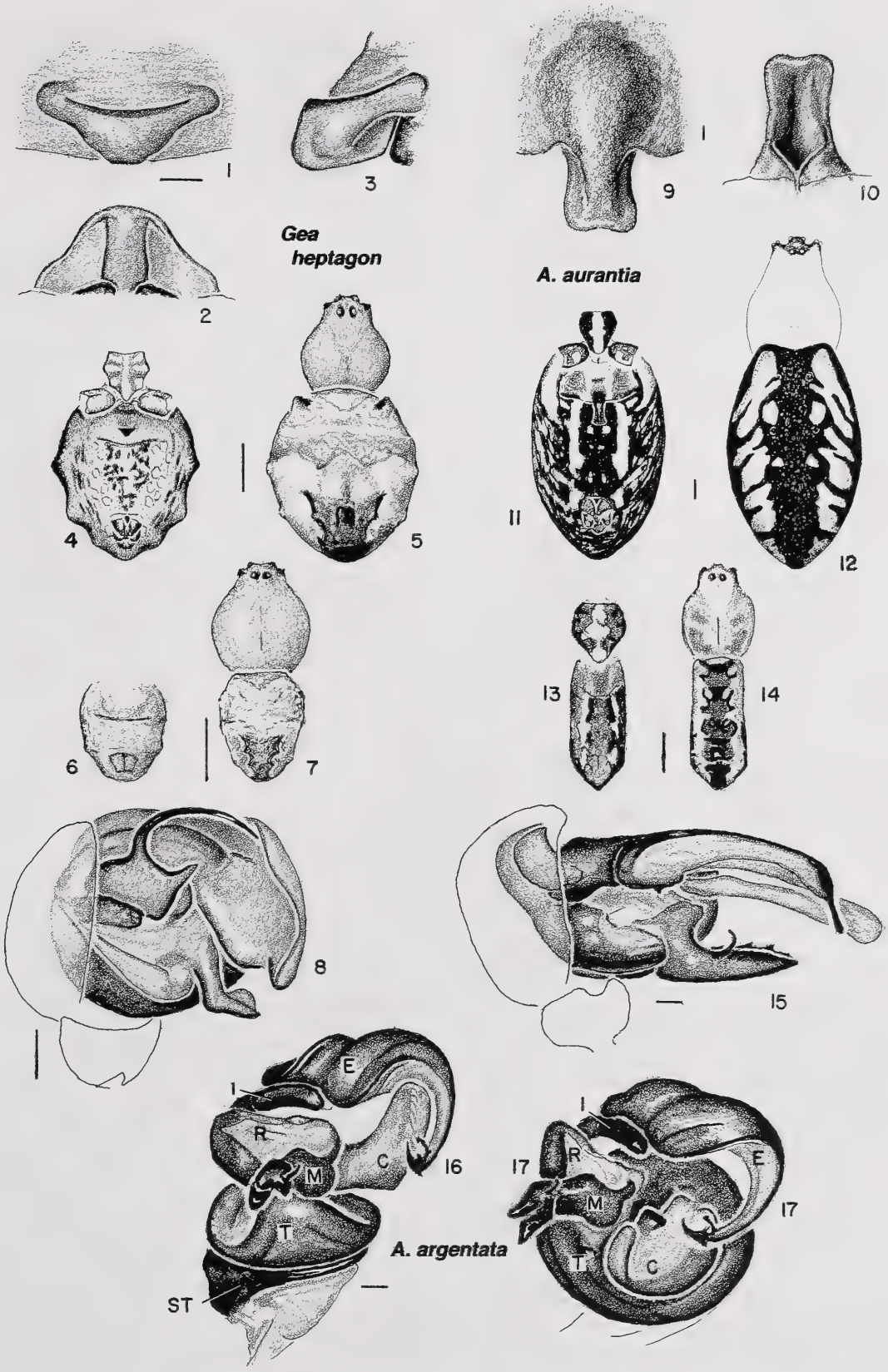
Argiope aurantia:—Levi, 1968: 338, figs. 43–57, ♀♂. Platnick, 2003.

Diagnosis. Females are separated by the black and yellow pattern of the abdomen (Fig. 12) and the distinct genitalia, a posteriorly directed prong (Figs. 9, 10). The male is colored as in the female (Fig. 14) and has a projecting embolus and conductor (Fig. 15). The genitalia of *A. aurantia* are closest to the Eurasian *Argiope bruennichi* (Scopoli), which differs by having abdominal coloration resembling that of *A. trifasciata* (Fig. 22) (Roberts, 1995).

Variation. Total length of females 15–32 mm, males 5.5–9.9 mm. The largest females come from southern U. S. and Mexico. In southern Mexico, the median dark band on the dorsum of the abdomen is broken by transverse yellow and black bands. The female illustrated (Figs. 9, 10) came from Veracruz, Mexico; the male (Figs. 13–15) from Georgia.

Distribution. Southeastern Canada to Guatemala (Map 1C).

Additional Records. UNITED STATES, MASSACHUSETTS *Barnstable Co.*: Quisset (USNM). *Hampshire Co.*: Amherst (MCZ). *Middlesex Co.*: Weston (CAS). CONNECTICUT Goshen (USNM); Jordan (USNM); Mt. Carmel (USNM); New Britain (USNM); New Haven (USNM); Newington (USNM); Oxford (USNM); Woodmont (USNM). PENNSYLVANIA *York Co.*: 3.6 km W Ashville (USNM). MARYLAND *Prince Georges Co.*: Bladensburg (USNM); Priest Bridge (USNM); Forestville (USNM); Takoma Park (USNM). *Hyattsville Co.*: West Lanham Hills (USNM). DISTRICT OF COLUMBIA Washington (USNM); Smith's Isl. (USNM). OHIO *Crawford Co.*: Galion (USNM). VIRGINIA *Giles Co.*: (USNM). *Grayson Co.*: (USNM). *Rockbridge Co.* (USNM). KENTUCKY *Boone Co.*: Florence (CAS). NORTH CAROLINA *New Hanover Co.*: Wilmington (USNM). *Tyrrell Co.*: Lake Landing (USNM). TENNESSEE *White Co.*: Bon Air, 10.2 km W Cumberland Co. (USNM). *Giles Co.*: Pearisburg (USNM). SOUTH CAROLINA *Oconee Co.*: Chattuga Riv. 1.5 mi. S Russell Bridge (USNM). GEORGIA *Chatham Co.*: Rt. 95 (USNM). FLORIDA *Alachua Co.*: Gainesville (USNM). *Bradford Co.*: Starke (USNM). *Dade Co.*: Lemon City (USNM). *Duval Co.*: Jacksonville (CAS). *Hillsborough Co.*: Tampa (USNM). *St. Lucie Co.*: Ft. Pierce (USNM). MICHIGAN *Oakland Co.*: Birmingham (CAS). *Wayne Co.*: Detroit (CAS). WISCONSIN *Dodge Co.* (USNM). *Marathon Co.* (USNM). *Winnebago Co.*: Oshkosh (USNM). ILLINOIS *Richland Co.*: Olney (USNM); Centerville (USNM). MINNESOTA *Wabasha Co.*: 4.8 km SE Kellogg (USNM). IOWA *Woodbury Co.*: Sioux City (USNM); Morningside (USNM). *Dickinson Co.*: Spirit Lake (USNM); Lake Okoboji (USNM). MISSOURI *Travis Co.* (CAS). *Phelps Co.*: Rolla (CAS). ARKANSAS *Conway Co.* (CAS). LOUISIANA *Ascension Par.*: Donaldsonville (CAS). *New Orleans Par.*: Harahan (USNM). *Orleans Par.*: New Orleans (USNM). TEXAS *Bastrop Co.*: 21 km SSE Elgin (USNM); 16 km NW Bastrop (USNM). *Bell Co.* (USNM). *Bexar Co.*: 16 km N San Antonio (CAS); San Antonio (CAS); Fort Sam Houston (CAS); Lackland Air Force Base (CAS). *Dallas Co.*: Dallas (USNM). *Harris Co*: 3.2 km W of Alief (CAS). *Leon Co.*: SW Marques (USNM). *Travis Co.*: Austin (CAS); 8 km SE Manor (USNM); Austin (USNM). *Victoria Co.*: Victoria



Figures 1–8, *Gea heptagon* (Hentz). 1–5, Female. 1–3, epigynum. 1, ventral. 2, posterior, 3, lateral. 4, sternum and abdomen, ventral. 5, dorsal. 6–8, male. 6, abdomen, ventral, 7, dorsal. 8, left palpus.

Figures 9–15, *Argiope aurantia* Lucas. 9–12, Female. 9, 10, epigynum. 9, ventral. 10, posterior. 11, sternum and abdomen, ventral. 12, dorsal. 13–15, male. 13, sternum and abdomen, ventral. 14, dorsal. 15, palpus.

Figures 16–17, *A. argentata* (Fabricius), male, left palpus, expanded. Scale lines, 1.0 mm, genitalia, 0.1 mm.

Abbreviations: C, conductor; E, embolus; I, stipes; M, median apophysis; R, radix; ST, subtegulum; T, tegulum.

(USNM). CALIFORNIA *Alameda Co.*: Oakland (CAS). *Los Angeles Co.* (USNM). *Marin Co.*: Lake Bon Tempe (CAS); San Anselmo (CAS). *Monterey Co.*: Salinas (USNM). *San Mateo Co.*: Daly City (CAS); Menlo Park (USNM). MEXICO *Tamaulipas*: Paso del Abra, 22°37′N, 99°1′W (AMNH). *Nuévo Léon*: Villa de Santiago Las Ajuntas, 1,300 m elev. (MCZ). *Nayarit*: 11.7 km E San Blas (CAS); 3.2 km N Sayulita, 19 Nov. 1976, ♀ (D. D. Wilder, CAS). *Jalisco*: Chamela, 16 Oct. 1988, ♀ (Buickerood, E. S. Ross, CAS). *Veracruz*: Alto Lucera, 18°7′N, 94°50′W, 10 Aug. 1966, ♀ (J., W. Ivie, AMNH).

BAHAMA ISLANDS South Bimini, ♀ (AMNH); Bimini, 30 Sep. 1947, ♀ (J. Oliver, AMNH).

Argiope trifasciata (Forskål)
Map 1B; Figures 18–26

Aranea trifasciata Forskål, 1775: 86. Holotype from Cairo, Egypt, lost.

Argiope trifasciata:—Thorell, 1873: 519. Levi, 1968: 340, figs. 58–72, 74–91, ♀♂. Platnick, 2003.

Diagnosis. Females can be separated from other American *Argiope* by the transverse dorsal lines on the abdomen, two longitudinal ventral lines (Fig. 21), and lack of posterior tubercles on the abdomen. It also differs in that the anterior, transverse lip of the epigynum lacks an anterior edge, present in all species with a similar epigynum (arrow, Fig. 18). The abdomen is similar to that of *A. bruennichi* of Eurasia, but *A. bruennichi* has an epigynum like that of *A. aurantia*.

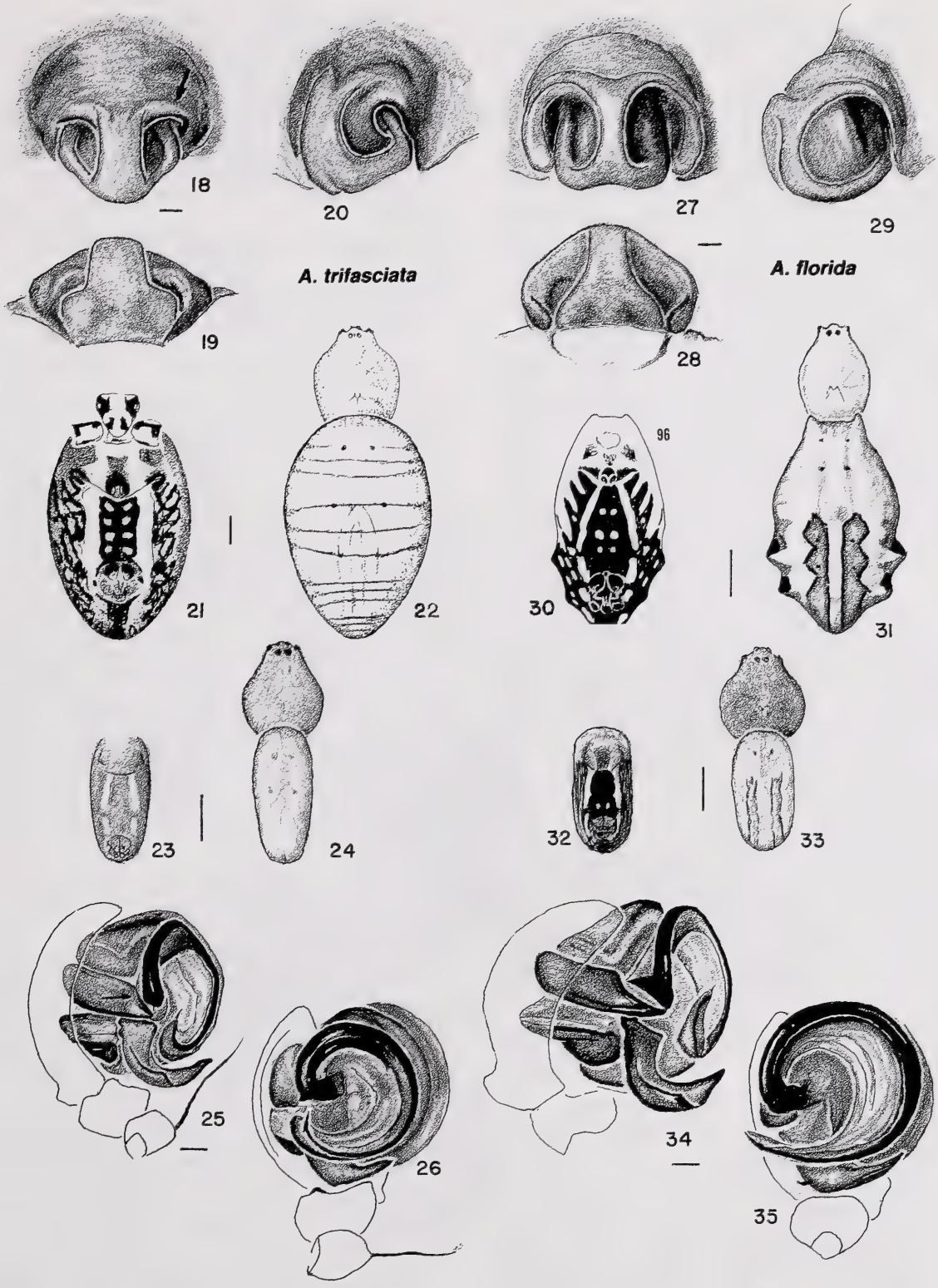
The male palpus differs from others with a similar palpus by having a joint between the embolus and the very large stipes (arrow, Fig. 25), as is also found in *A. florida* (Fig. 34). *Argiope trifasciata* differs from *A. florida* (Fig. 35) in having a smaller embolus circle in ventral view (Fig. 26), still showing stipes to the left and the tegulum on the right (if the left palpus is viewed as in Fig. 26).

Variation. Total length of females 10.3–21.0 mm, males 3.8–7.3 mm. Abdomen variable, rarely with transverse grooves, sometimes with a tail (Levi, 1968). A female and males from Costa Rica were used for Figures 18–20, and 23–26.

Distribution. Cosmopolitan, but absent from Europe. (American distribution, Map 1B.)

Additional Records. UNITED STATES, MAINE *Washington Co.*: Lubec, Moosehorn Natl. Wildlife Refuge (MCZ). MASSACHUSETTS *Barnstable Co.*: Teaticket (USNM). *Dukes Co.*: Nashawena Isl. (C. Parsons, MCZ). Penikese Isl. (MCZ). *Nantucket Co.*: Nantucket, Almanach Pond (USNM). CONNECTICUT Cheshire (USNM); Colchester (USNM); Goshen (USNM); Monroe (USNM); New Britain (USNM); Newington (USNM); Rocky Hill (USNM); South Meriden (USNM); Storrs (USNM). NEW YORK *Madison Co.*: Lebanon (USNM). PENNSYLVANIA *York Co.*: W Ashville (USNM). DISTRICT OF COLUMBIA (USNM). WEST VIRGINIA *Pocahontas Co.*: Watoga State park (USNM). *Tucker Co.*: Canaan Valley State Park (USNM). OHIO *Portage Co.*: 8 km ESE Ravenna, 41°8.5′N, 81°90′W (CAS). VIRGINIA Allegheni Mts., Hone Quarry Camp (USNM). *Montgomery Co.* (USNM); Blacksburg (USNM); Shawsville (USNM). *Grayson Co.*: Galax (USNM). NORTH CAROLINA *Allegheny Co.*: Sparta (USNM). WISCONSIN *Dane Co.*: Madison (USNM). *Oconto Co.*: (USNM). IOWA *Clarke Co.*: Osceola (USNM). *Woodbury Co.*: Sioux City (USNM). MISSOURI *Vernon Co.*: 24 km S Nevada, from mud dauber nest (MCZ). NORTH DAKOTA *Slope Co*: vic. Burning Coal Mines (AMNH). KANSAS *Pottawatomie Co.*: Onaga (USNM). NORTH DAKOTA Slope (USNM). ARKANSAS *Lawrence Co.*: Imboden (USNM). OKLAHOMA *Woods Co.*: Alva (USNM). TEXAS *Bell Co.*: Paire Dell (USNM). *Burleson/Lee Cos.*: Yegua Creek, NE Giddings (USNM). *Burnet Co.*: Sycamore Creek, 16 km ENE Marble Falls (USNM). *Denton Co.*: Lake Dallas (MCZ). *Travis Co.*: Austin (USNM); 3.2 km W Manor (USNM). COLORADO *Boulder Co.*: Boulder (USNM). ARIZONA *Santa Cruz Co.*: Sycamore Canyon (MCZ). WASHINGTON *Benton Co.*: 8 km N Prosser (USNM). *Chelan Co.*: Lake Chelan, 47°88′N, 120°8′W (USNM). OREGON *Umatilla Co.*: Pendleton (CAS). CALIFORNIA (USNM). *San Diego Co.*: San Diego (AMNH); Del Mar (USNM). MEXICO *Tamaulipas*: 24 km S Victoria, 23°38′N, 99°12′W, 22 July 1966, ♀ (J., W. Ivie, AMNH). *Chihuahua*: 25.6 km NNW Chihuahua, 28°47′N, 106°10′W, 8 Sep. 1964, ♀ (J., W. Ivie, AMNH). *Baja California Sur*: 4.8 km NW San Antonio, 13–18 Dec. 1977, ♀ (L. Vincent, C. Griswold, CAS). *México*: 38 km NW Mexico City, 6 June 1948, ♀ (AMNH). *Oaxaca*: nr. San Gabriel, 900 m, N Puerto Escondido, S of Oaxaca, 1963, ♀ (C. M. Bogert, AMNH). *Yucatan*: Uxmal, 29 Sep. 1959, ♂ (O., I. Degener, AMNH); Chichen Itza, Feb. 1934, ♂ (AMNH). COSTA RICA *Guanacaste*: Palo Verde, ca. 27 km SSW Bagaces, Jan. 1978, ♀♂ (W. Eberhard, MCZ).

BAHAMAS Hatchet Bay, Eleuthera Isl., 2 Apr. 1953, ♀♂ (Hayden, Giovannoli, AMNH). HAITI Furcy, Nov. 1942, ♀ (R. Curtiss, USNM). VIRGIN ISLANDS St. Thomas, ♀ (ZMK). ANTIGUA June 1918, ♀ (Univ. Iowa Exped., USNM). WEST ANTIGUA nr. Jolly Beach, 2 July 1963, ♀; 20 Sep. 1963, ♀ (E. N. Kj.-Waering, AMNH).



Figures 18–26, *Argiope trifasciata* (Forskål). 18–22, female. 18–20, epigynum. 18, ventral. 19, posterior. 20, lateral, 21, sternum and abdomen, ventral. 22, dorsal. 23–26, male. 23, abdomen, ventral. 24, dorsal. 25, 26, palpus. 25, mesal. 26, ventral.

Figures 27–35, *Argiope florida* Chamberlin and Ivie. 27–31, female. 27–29, epigynum. 27, ventral. 28, posterior. 29, lateral, 30, abdomen, ventral. 31, dorsal. 32–35, male. 32, abdomen, ventral. 33, dorsal. 34, 35, palpus. 34, mesal. 35, ventral.

Scale lines, 1.0 mm, genitalia, 0.1 mm.

SURINAME Matapica Beach, 4 Oct. 1962, ♂ (B. Malkin, AMNH). COLOMBIA *Antioquia*: Belmira Paramo, 3,150 m, 12 Apr. 1988, ♀ (M. A. Serna, MHNM). *Cundinamarca*: Monterredondo, 1,200 m, 25 Feb. 1975, ♂ (P. A. Schneble, MCZ). *Valle*: Buena Ventura, 4 Nov. 1950, ♀ (E. S. Ross, CAS); Jamundi, Oct. 1991, ♀ (A. Batista, MCP 2861). PERU *Ancash*: nr. Colca, Río Fortaleza, 2,150 m, 1 Oct. 1956, ♀ (W. Weyrauch, CAS). *Ayacucho*: Ayacucho, Jan. 1967, ♀ (T. A. Galarza, IBSP). *Cuzco*: Machu Picchu, 2,600–2,800 m, 1–5 July 1964, ♀ (B. Malkin, AMNH); 24 Feb. 1971, ♀ (W. D. Wood); 24 Jan. 1973, ♀ (A. Moreton, MCZ); 2,400 m, 16 Oct. 1987, ♀ (J. Coddington, USNM). BRAZIL *Amapá*: Macapa, nest of *Eumenes,* June 1966, ♂ (Becker, MACN). *Espírito Santo*: Ilha da Trinidade, 1992, 1995, ♀ (R. Castelli; D. Lewis, MCP 1675, 6144, 6145, 7600). *Mato Grosso*: Porto Cercado, 2 Aug. 1992, ♂ (G. A. Braul, MCP 2486); Santa Antonio de Levergene, 6 Oct. 1991, ♂ (M. I. Marques, MCP 2557). *Mato Grosso do Sul*: Anaurilândia, 22°22′S, 52°48′W, 15 Nov.–23 Dec. 1998, ♀ (IBSP). *São Paulo*: Presidente Epitácio, 16 Jan.–13 Feb. 1999, ♀♂ (IBSP); São Paulo, 14 July 1995, ♀ (C. M. P. Nascimentó, IBSP). *Rio Grande do Sul*: Capão Novo, 1992, ♂ (C. Mazzilo, MCP 4606); Itapuã, Porto Alegre, 4 Feb. 1975, ♂ (A. Lise, MCN 02450); Santa Maria, Apr. 1988, ♀ (A. A. Lise, MCP 4897); 16 Mar. 1990, ♀ (D. Linck, MCP 6016). URUGUAY 1913, ♀ (Copuelo, MACN). PARAGUAY Feb. 1945, ♀ (J. Cranwell, MACN); Isla Yasilen, Nov. 1975, ♂ (A. Martins, MACN). *Paraguari Prov.*: Ybycui, 27 May 1980, ♀ (P. J. Spangler, USNM). ARGENTINA *Misiones*: Pto. Aguirre, 1943, ♀ (J. M. Viana, MACN); Santa María, Oct. 1944, ♀ (J. M. Viana, MCN); Pto. Iguazú, Dec. 1959, ♀ (MCN). *Formosa*: Palo Santo, ♀ (H. Hepper, MACN). *Chaco*: Agua de Oro, ♀ (Apóstol-Tonina, MACN); Resistencia, July 1934, ♀ (J. B. Daguerre, MCN); Basail, ♀ (M. Birabén, MLP 15116). *Corrientes*: Corrientes, Jan. 1949, ♀ (J. Lieberman, MACN); Solari, ♀ (M. Birabén, MLP 16559); Manantiales, ♀ (Apóstal, MCN); Apipé, 1945, ♀ (W. Hanke, MACN). *Entre Ríos*: Diamante, 19 Mar. 1918, ♀ (A. G. Frers, MCN); Villaguay, 26 Apr. 1918, ♀ (A. G. Frers, MCN). *Santa Fé*: Las Gamas, 20 km W Vera, Oct. 1994, ♂ (M. Ramírez et. al., MACN); 9 July 1945, ♀ (E. Aiello, MACN); Tostado, 1944, ♀ (A. Giai, MACN); Aug. 1945, ♀ (MCN); Mar. Chiquita, May 1962, ♀ (C. Hepper, MACN). *Córdoba*: Calamuchita, Dec. 1940, ♀ (J. M. Viana, MACN); Leones, 5 Feb. 1946, ♀ (MACN); Agua de Oro, Mar. 1940, ♀ (J. A. de Carlo, MACN). *San Luis*: Villa Elena, Oct. 1974, ♂ (J. M. Viana, MACN). *Buenos Aires*: Buenos Aires, ♀ (Zotta, MACN); Pergamino, Mar. 1963, ♀ (Sucro, MACN); Zekya, 3 Mar. 1935, ♀ (MACN); Bella Vista, 11 Mar. 1984, ♀ (J. M. Gallardo, MACN). *La Pampa*: General Pico, Mar. 1975, ♀ (J. Williamson, MACN). CHILE *Reg. Metropolitana*: Talagante, 15 Dec. 1974, ♀, 18 Sep. 1975, ♀ (L. Berrios, AMNH); Conchali, Santiago, 1 Feb. 1972, ♀ (I. Maller, AMNH); Antumapu, Mar. 1973, ♀ (MCZ); El Monte, 27 Feb. 1973, ♂ (MCZ); Lampa, May 1979, ♀ (L. Peña, AMNH); Quilicura, 1979, ♀ (L. Peña, AMNH). *Arauco*: Angol, 1950, ♀ (D. S. Bullock, CAS). *Ñuble*: Chillan, 10 Apr. 1976, ♀ (G. Moreno, MCZ); Puente Río Cato, 26 Mar. 1981, ♀ (G. Moreno, MACN). *Llanquihue*: Llanquihue, Mar. 1942, ♀ (Lieberman, MACN). JUAN FERNANDEZ ISL. Más Afuera, Cerro Inocentes, 1,000 m, 18 Mar. 1962, ♀ (B. Malkin, AMNH).

HAWAII Oahu, 1961, ♀ (O., I. Degener, AMNH).

Argiope florida Chamberlin and Ivie
Map 1D; Figures 27–35

Argiope florida Chamberlin and Ivie, 1944: 95, figs. 93, 94, 96, ♀. Female holotype from Lake Worth, Florida, lost, not examined. Levi 1968: 344, figs. 92–111, ♀♂. Platnick, 2003.

Diagnosis. Females of *A. florida,* as well as *A. trifasciata,* differ from females of *A. argentata, A. blanda,* and *A. savignyi* by having a pair of longitudinal white bands on the black venter of the abdomen (Fig. 30). They differ from *A. trifasciata* by the dorsal coloration and shape of the abdomen. Dorsally, there is a pair of longitudinal bands (Fig. 31), and the sides of the abdomen have tubercles (Fig. 31). The epigynum, unlike that of *A. trifasciata,* has a lip on the anterior rim of the epigynum (Fig. 27).

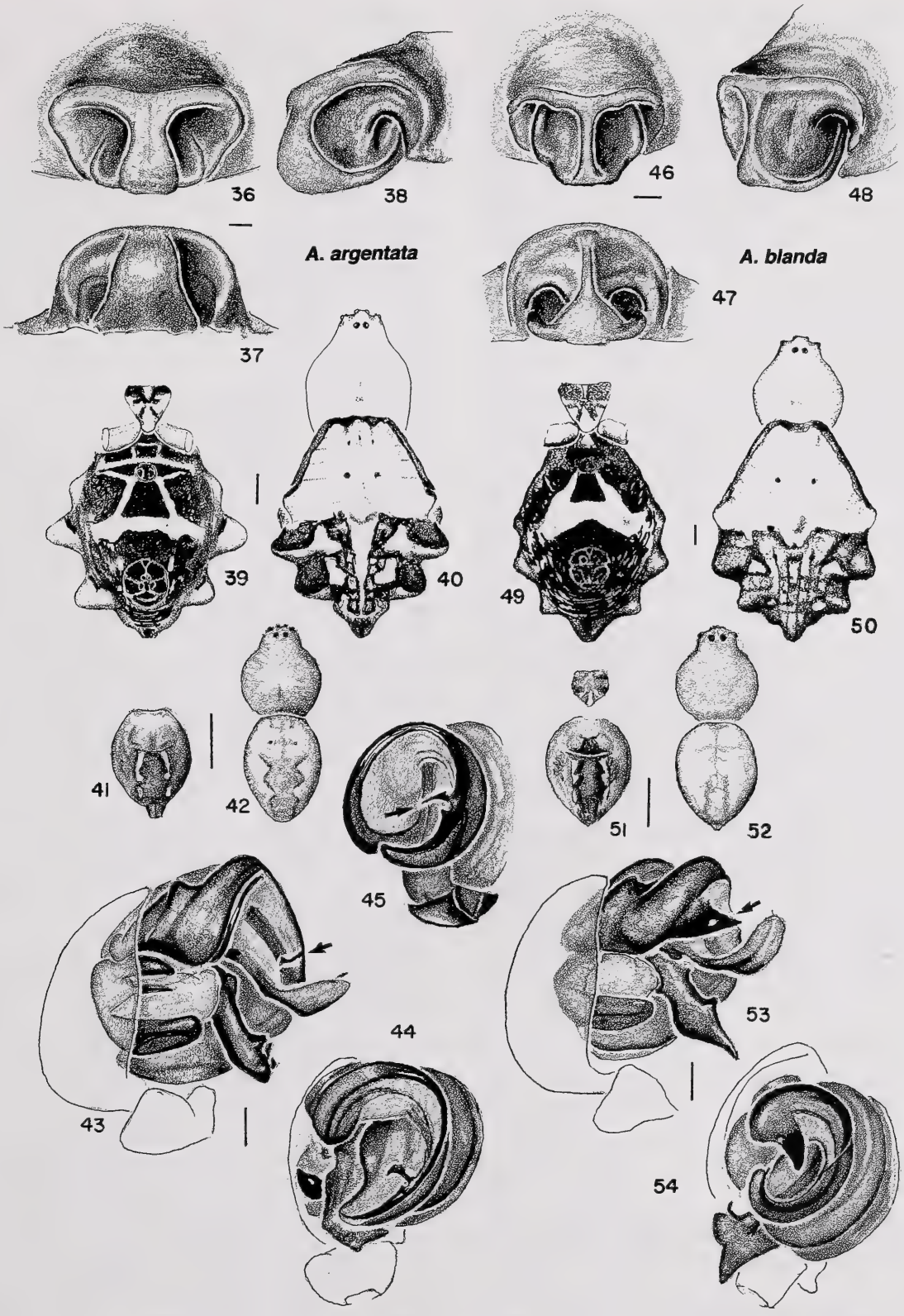
Males differ from most *Argiope*, except *A. trifasciata*, by having a joint between the embolus and stipes in the palpus (arrow, Fig. 25). They differ from *A. trifasciata* in having the embolus longer and with a wider circle. The embolus coil covers both the tegulum and stipes on each side if viewed face on (Fig. 35).

Variation. Total length of females 12.5–18.0 mm, males 5.1–6.7 mm. The illustrations (Figs. 27–29, 31) were made from a female from Georgia, the male (Figs. 32–35) from Florida.

Natural history. Spiders were collected between trees in open pine scrub on sand at 1 m height by F. Enders in North Carolina.

Distribution. North Carolina to Florida; west to Louisiana, Arizona (Map 1D).

Additional records. UNITED STATES, NORTH CAROLINA *Bladen Co.*: 13 km S White Lake, 22



Figures 36–45, *Argiope argentata* (Fabricius). 36–40, female. 36–38, epigynum. 36, ventral. 37, posterior. 38, lateral, 39, sternum and abdomen, ventral. 40, dorsal. 41–45, male. 41, abdomen, ventral. 42, dorsal. 43–45, left palpus. 43, mesal. 44, ventral. 45, subventral.

Figures 46–54, *Argiope blanda* O. P.-Cambridge. 46–50, female. 46–48, epigynum. 46, ventral. 47, posterior. 48, lateral, 49, sternum and abdomen, ventral. 50, dorsal. 51–54, male. 51, sternum and abdomen, ventral. 52, dorsal. 53, 54, palpus. 53, mesal. 54, ventral.

Scale lines, 1.0 mm, genitalia, 0.1 mm.

Aug. 1970, 11♀ (F. Enders, MCZ). *Hanover Co.*: Carolina Beach, Wilmington, 27 Aug. 1932, 1♀ (A. M. Chickering, MCZ). GEORGIA *Richmond Co.*: Augusta, 18 Aug. 1944, 1♀ (P. W. Fattig, AMNH). FLORIDA *Broward Co.*: Fort Lauderdale, Sep. 1932, 1♀ (M. Bates, MCZ). *Highlands Co.*: Rt. 70, 3.2 km E Rt. 27, Aug. 1963, 1♀ (T. Eisner, MCZ). *Lake Co.*: Altoona, 1♂ (N. Banks, MCZ). *Liberty Co.*: 18–20 Aug. 1960, 1♀ (J. McCrone, MCZ). *Marion Co.*: 14 Aug. 1959, 1♀ (J. McCrone, MCZ). LOUISIANA *Cameron Par.*: Cameron, 1♀ (N. Banks, MCZ).

Argiope argentata (Fabricius)
Map 2A; Figures 16, 17, 36–45

Aranea argentata Fabricius, 1775: 433. Type specimens from the Indies [West Indies] lost.
Argyopes argentata:—C. L. Koch, 1839: 38, pl. 361.
Argiope argentata:—Levi, 1968: 345, figs. 42, 73, 112–136, ♀♂. Platnick, 2003.

Diagnosis. Females of *A. argentata* can be separated from similar species *A. blanda* and *A. savignyi* by the coloration of the abdomen (Fig. 40), especially by the relatively narrow, transverse white line on the venter of the abdomen (Fig. 39).

Males have a spur on the tip of the embolus (arrow, Figs. 43, 45), usually sclerotized, black and easy to see, not found in any other *Argiope*.

Variation. Total length of females 6.2–18.8 mm, males 2.8–5.2 mm. The smallest females, those less than 8 mm total length, mostly from the Amazon area, have the dorsal pattern of the abdomen as in *A. florida*, with two longitudinal stripes and the coloring of an immature, but have the epigynum containing broken off embolus tips of a male of *A. argentata*.

The illustrations of the female (Figs. 36–38) were made from a specimen from Colombia, the male (Figs. 41–45) from Minas Gerais, Brazil.

Distribution. Southern Florida, California to Argentina and northern Chile (Map 2A).

Additional Records. UNITED STATES, FLORIDA *Monroe Co.*: Greyhound Key (CAS); Key West (USNM); Aiken, Key Largo (USNM). TEXAS *Cameron Co.*: Brownsville (USNM); Port Isabel (USNM). CALIFORNIA *San Joaquin Co.*: Clemente, 3 May 1887, ♀ (USNM). *Contra Costa Co* (AMNH). *San Obispo Co*: Cuyama River at Santa Barbara Co. line (CAS). *Los Angeles Co*: San Clemente Isl. (AMNH). *San Diego Co.*: La Jolla (CAS); Torrey Pines, La Jolla (USNM); San Diego (USNM); Del Mar (USNM). MEXICO *Tamaulipas*: 24 km S Victoria (AMNH); 19 km SE Victoria (AMNH); NE of Pedilla, 24°3′N, 98°43′W (AMNH); 8 km S Tres Palos, 24°28′N, 98°20′W (AMNH); 21 km N Aldama (CAS); nr. Altamira (USNM); Río Cherreras, 24°N, 98°W (AMNH). *Sonora*: 11 km N El Desemboque (CAS). *Baja California Norte*: 19 km S Punta Calaveras (AMNH); Isla San Martín (CAS); Isla de Cedros (CAS); Lion Cove (CAS); Isla Natividad (CAS). *Baja California Sur*: Bullenas Bay (USNM); Isla Partida (CAS); 8 km S Miraflores road to Las Casitas (CAS); 5 km NW San Antonio (CAS); Santa Margarita, sand dunes, 3 km W Puerto Cortes (CAS); 24 km W El Crucero (CAS); Isla Magdalena (CAS); St. Margarita Isl. (USNM). *Sinaloa*: 3.2 km S Elota, 23°55′N, 106°48′W (AMNH); Mazatlán (CAS); 8 km NW Mazatlán (CAS). *Nayarit*: San Blas, Mantauchen Beach (AMNH, CAS). *Guerrero*: 3.6 km N Millipanias (AMNH); Acapulco (AMNH). *Veracruz*: 8 km S Veracruz, 19°8′N, 96°8′W (AMNH); Veracruz (AMNH, CAS, MCZ); betw. Veracruz and Alvarado (AMNH). *Tabasco*: coast (CAS). *Campeche*: Chicanna ruins, ca. 8 km W Xpujil, 89°31′W, 18°32′N (MCZ). *Yucatan*: Chichen Itza (AMNH). *Quintana Roo*: 50 km S Cancún (CAS); Islas Revilla Gegido, I. Carión (AMNH). HONDURAS Roatan Isl., French Harbour (AMNH). COSTA RICA *Limón*: Hacienda de Limón (USNM). *Cartago*: Turrialba (AMNH). *Puntarenas*: (USNM). PANAMA *Bocas del Toro*: Río Changuila, Corriente (MCZ). *Chiriquí* (AMNH). *Panamá*: Barro Colorado Island (AMNH, MCZ); Balboa (AMNH); Frijoles (USNM); Canal Zone Forest [Soberiana Natl. Park] (MCZ); Soberiana Natl. Park, Pipeline Road (USNM); Cerro Azul (CAS); Cerro Campana (AMNH); Summit (AMNH); Gamboa (AMNH); Madden Dam (AMNH); 7–14 km N El Llano (CAS); Panamá City (CAS); Paraíso (USNM).

WEST INDIES Very common on smaller Islands, also Jamaica, Puerto Rico, few records from Cuba and Hispaniola.

VENEZUELA *Delta Amacuro*: Canon Jobure (AMNH). *Sucre*: Cumana (MCN 2689). *Monagas*: Caripito (AMNH). *Bolívar*: 64 km N Guesipati (USNM). *Dist. Federal*: Caracas (USNM); *Aragua*: M. Pittier Natl. Park, Rancho Grande (AMNH, FSCA, USNM). *Miranda*: 34 km N Altagracia, Guatopa Natl. Park (AMNH). *Guárico*: Hato Masaquarai, 8°34′N, 67°35′W, 60 m (MCZ); Parque Nacional Aquara-Guariquito (MCN 21345). *Carabobo*: San Esteban (AMNH). *Amazonas*: Neblina Massif, 12.5 km NNW of Pico Phelps, 1,670–1,690 m, 0°54′N, 66°2′W (MCZ); 2.8 km NE Pico Phelps 0°49′N, 65°59′W, 2,100 m (AMNH). *Zulia*: Maracaibo (AMNH); nr. Rosario (FSCA). GUYANA Georgetown (AMNH); Sauri-Wau River (AMNH); Isher-tun, 16 km E Rupununi River (AMNH); nr. Yupukarri, Rapununi River (AMNH). *Mazaruni/Potaro*: Takutu Mts., 6°15′N, 59°5′W (USNM). SURINAME *Marowijne*: Christian Kondre (AMNH); Mangaman Kondre (AMNH, MZSP 5511); Christian Kondre (B.

Malkin); Paramaribo Agr. Sta. (AMNH, MCZ); Matapica Beach (AMNH); Voltzberg-Raleighvallen Nature Reserve, Saramanca, 4°32′N, 56°33′W (MCZ). FRENCH GUIANA St. Laurent du Maroni (AMNH). *Cayenne*: Montagnes Kaw, nr. Camp Calman, 27 km SE Roura, 4°33′N, 52°0′W (USNM). COLOMBIA *Bolívar*: Rio Frío (AMNH); Cartagena to Bocagrande (CAS). *Santander*: Río Suarez (AMNH). *Boyacá*: Muzo (MCZ). *Antioquia*: Amaga, 1,400 m (MCZ); Mutatá (MCZ); Medellín (MCZ); Santa Fé de Antioquia, 700 m (MCZ); La Estrella, 1,700 m (MCZ); El Peñol, 2,100 m (MCZ); El Santuario, 2,150 m (MCZ). *Cundinamarca*: Monterredondo, 1,300 m (MCZ). *Meta*: ca. 20 km N Rio Muco, 20 km S el Porvenir, Finca Chenevo, 170 m (MCZ); Puerto Lleras, Lomalinda, 3°18′N, 73°22′W (CAS). *Huila*: Parque Arqueológico de San Augustín (CAS). *Valle*: Buga (CAS); Cali, 1,000 m (MCZ) 29 km W Cali (MCZ); Palmira (CAS); Finca Iberia (MCP 2860). *Cauca*: Popayán (CAS). *Nariño*: Boca Grande (SMNK 3048); Junin, 140 m (SMNK 3052); Barbacoas (SMNK 1937); nr. Consaca, 1,700 m (SMNK 3049); El Pepino (SMNK 3099). *Putumayo*: road from Puerto Lima to Santa Lucia, 240 m (SMNK 3059); Puerto Asis (SMNK 3100). ECUADOR Xapatal (CAS). *Esmeraldas*: 11 km SE of Lorenzo, La Chiquita (MCZ). *Napo*: 20 km E Puerto Napo, Alinahuí, 1°0′S, 77°75′W (CAS); Via Acua, 55 km S Coca (CAS). *Pichincha*: Pera (MACN); 17 km SE Santo Domingo (AMNH). *Pastaza*: 3–13 km N Puyo, 953 m (CAS); 12 km W of Puyo (USNM). *Tungurahua*: Río Topo (CAS); Baños, 1,800 m (AMNH, CAS, USNM). *Guayas*: Macuchi (CAS); 3.2 km NE La Libertad (CAS); 3.2 km S Manglaralto (CAS); Manta (CAS); Guayaquil (CAS). GALAPAGOS ISLANDS Tower Isl. (AMNH); Isla Santa Cruz, Darwin Research Station (CAS); Indefatigable Isl. (CAS); Conway Bay (USNM); Albemarle Isl. (CAS); Elizabeth Bay (USNM); Isla Isabela (CAS); Chatham Isl. (USNM); Baltra Isl. (USNM). PERU *Loreto*: Río Momón, nr. Iquitos (CAS); Río Mamore nr. Iquitos (CAS); Parinari Canyon, Río Samiria (AMNH). *Amazonas*: Montenegro, Bagua (AMNH). *Piura*: Cerra Prieto (CAS); Sechura (CAS); Sullana (CAS); Cabo Blanco (CAS); El Muerto (CAS). Puñapí (CAS); Negritos (CAS); Quebrada Charanal (CAS). *Cajamarca*: Nanchoc Quebrada, 400 m, 6°57S, 79°15W (MCZ); San José de Lourdes, 1,200 m, 05°4′S, 78°54′W (CAS). *La Libertad*: El Alto (CAS). *Huánuco*: Huallaga Vall, Cucharas (CAS); Huaquareo, Río Huallaga, Paray, Cuchuras (CAS); Tocache, Rio Huallago, 670 m (CAS); Tingo María, 670 m (CAS); 98 km E Tingo María (CAS). *Lima*: 8 km NE Pucusana (CAS); Barranco (CAS); Ventanilla, 40 km N Lima (MZSP 8233). *Ayacucho*: Huanta, 2,400 m (CAS); 16 km N Huanta, nr. Río Mantaro (CAS); Río Pampas, Hwy. 7 (CAS). *Cuzco*: Machu Picchu (AMNH, USNM). *Arequipa*: Magía (MCZ); Atiquipa, Chala, 200 m (CAS); Chala, 300 m (CAS); Atico (AMNH); Alto Q. del Toro, S Camana (AMNH). *Tacna*: S Camiara (AMNH); Las Yaras (AMNH). BRAZIL. *Pará*: Jacareacanga (AMNH); Belém (MACN, IBSP); Maritus, Ananindéua (AMNH); Rio Gurupi, Canindé (AMNH); Conceição do Araguaia (AMNH); Canuaná, Melgaço (MCP 9367); Pedras, Rio Cuminá (MZSP 13091). *Roraima*: Ilha de Maracá (MCP 1825); Rio Branco (IBSP). *Amazonas*: Manaus (CAS, MZSP 13090, SMNK 0064, 0065, 0066); 12 km NE Manaus, Itacoatiara Hwy. (AMNH); Reserva Ducke, Manaus, 2°55′12″S, 59°58′48″W (MCN 18386, 18387, SMNK 1931); Igarapé Belém nr. confluence with Rio Solimões (AMNH); Presidente Figueiredo (IBSP); Maturaca, São Gabriel da Cachoeira (MCP 1257, 1352); Uaupés (IBSP); Fonte Bôa (AMNH). *Acre*: Reserva Extrativista de Humaitá, 9°58′12″S, 67°48′36″W (SMNK 2013, 2023). *Maranhão*: Aldeia Yavaruhu, 50 km E Candidé, Pará (AMNH). *Ceará*: Ceará, Fortaleza (MCZ); Limoeiro do Norte (SMNK 1942); Nova Olinda, 7°5′24″S, 39°40′48″W (SMNK 1943). *Rio Grande do Norte*: Estação Ecólogica do Seridó, Serra Negra (IBSP); Natal (MZSP 13089); Macalbo (MZSP 5567). *Paraíba*: Independençia (MCZ); Represa da Farinha, Patos (IBSP). *Pernambuco*: between Catimbu Buíque (MCN 25576); Serra Negra (MCN 24956); João Pesso (IBSP); Recife (IBSP); Sitio São Miguel, São José da Mata (A. D. Brescovit, IBSP); Tappacurá (IBSP). *Alagoas*: São Miguel (MZSP 9540); Mangabeiras (MZSP 13088). *Sergipe*: Crasto, Santa Luzia do Itanhi (IBSP); São Cristovão (IBSP); Santa Luzia do Itanhi (IBSP); Barra dos Coqueiros (IBSP). *Bahia*: Galeão (ZMK); Bejoes (MCP 11886); Porto Seguro (MCN 28472); Toca Esperança Central (IBSP); Ilha Santa Bárbara, Arq. De Abrolhos (IBSP); Cabruçu, Ilhéus (IBSP); Tinedi, Central (IBSP); Barra do Mendes (IBSP); Pratinha Iraquara, 12°21′S, 41°32′W (IBSP); Parque Ipê, Feira de Santana (IBSP); Raso da Catarina (IBSP). *Tocantins*: Serra do Lageado, Palmas (MCN 28705). *Goiás*: Alto Paraíso (IBSP); Anápolis (MZSP 603); Aragarcas (MZSP 13 086); Santa Isabel do Morro, Ilha de Banalal (AMNH). *Mato Grosso*: Alta Floresta (IBSP); Barra do Tapirape (AMNH); Chavantina (MZSP 3928); 260 km N Xavantina, 12°49′S, 51°46′W, campo-grassland (MCZ); Chapada dos Guimarães (MCP 2162, 11572); San Antônio de Levergere (MCP 2409). *Mato Grosso do Sul*: Anaurilândia, 22°22′S, 52°48′W (IBUS); Morro do Azaite, Corumbá (IBSP); Paranaiba (IBSP). *Espírito Santo*: Guarapari (MZSP 9574); Linhares (MZSP 5308); 20 km N Linhares, Forest Reserve (CAS); Reserva da Aracruz Celulose, Linhares (IBSP); Reserva Florestal Vale do Rio Doce, São Marcos (IBSP); Rio Itabapuana, São José do Calçado (IBSP); San Gabriel Bay (CAS). *Rio de Janeiro*: Angra dos Reis (MZSP 5137); Ilha de Governador (MCN 9406); Leblon (AMNH); Mangaratia (AMNH); Ilha Marambaia (IBSP); Maricá (MZSP 15333, 15357, 15354, 15372, 15394); Mendes (MZSP 8073); Nova Iguaçu, Miguel Couto (AMNH); Petrópolis, 850 m (AMNH); Represa, Rio Grande (AMNH); San Antonio de Imbe, S. Maria (AMNH); São José, Rio Prêto (MZSP 1936); Silva Jardim (AMNH); Serinha (IBSP); Serra do Mandanha, 22°50′S, 43°34′W

(CAS); Teresópolis (USNM); Valença (MZSP 15536, 15537); Volta Redonda (IBSP). *Minas Gerais*: Coimbra (IBSP); Gov. Valadares, building rubble (AMNH); Horizonte (AMNH); Uberlândia (MCP 1986); Lavras (MCZ); Minas de Serinha Diamantina (AMNH); Pedra Azul (AMNH). *São Paulo*: Água Funda [?] (MZSP 4499); Americana (MZSP 4643); Amparo (MZSP 586, 4658); Baruerí (MZSP 5871); Boraceia (MZSP 3520, 4836, 4839, 5948, 8081 9323, 10511); Boraceia, Salesópolis (AMNH); Caraguatatubo (MZSP 4689, 4804); Cocaia, Represa Nova (MZSP 4647, 9767); Corumbataí (IBSP); Cotia (IBSP); Guanabara (MZSP 3238, 4010); Ibitu (MZSP 6755); Ilha Quelma de Grande (IBSP); Ilha S. Sebastian (MZSP 8082); Itararé (IBSP); Mairiporã (MZSP 5673); Mogi das Cruzes (MZSP 4618); Nazaré Paulista (IBSP); Nova Europa (MCN 3950; MZSP 4329, 5313); Osasco (IBSP); Pindamonhangaba (IBSP); Piracicaba (IBSP); Ribeirão Preto (IBSP); São Paulo (IBSP, MZSP 148, 4648, 6743, 8078, 8084); Camino de Mar, 33 km S São Paulo (MCZ); Ipiranga (MZSP 3124, 6867); São Sabastião (MZSP 4457, 9757); Serra Bocaina (MZSP 5754); Ubatuba, Praia de Lázaro (MCN 17416); Parque Estadual da Serra do Mar, Ubatuba, Picinguaba (IBSP); Vila Mercedes [?] (MZSP 6646). *Paraná*: Chac. S Manoel, Cachoeíva (IBSP); Corupa (AMNH); Curitiba (IBSP); Iguaçu, forest along shore (MCN 21836, MCZ); Parque Estadual do Cerrado, Jaguariaina (IBSP); Pilar do Sul [?] (MZSP 6548); Rio Jaguaçú, Salto Caxias, Capitão Leonidas Marques (MCN 23450); São Luis do Purunã (MZSP 7023); Villa Velha [?] (MZSP 7850). *Santa Catarinha*: Palhoça (IBSP); Pinhal (AMNH); São Domingos (MCP 11352). *Rio Grande do Sul*: Alvorade (MCP 1576); Bom Jesus (MCN 17397, 29291); Cacapava de Sul (MCP 1438); Capoa da Genova, Capoa Nova (MCP 3139); 116 km 124 Camaquã (MZSP 7000); Caxias do Sul (MCP 11776); Cidreira (MCP 2240); Cruz Alta (F. Silveira, MCN 4380); Erechim (MCN 19572); Erval Grande (MCP 1556, 4452); Guaíba (MCN 14418, MCP 4843, 7546, 7403, 7547); Montenegro (MCN 7153, 7154); Nova Milano Farroupilha (MCP 3097); Pelotas (AMNH); Porto Alegre (MCN 3834, 15901, 3543, MCP 1031, 1039, 0062, 2691, 0463); Br. 116, Porto Alegre-Pelotas, R. 3 (MZSP7570); Santa Maria (MCN 4004, 4894, 6013, 6014, 6015, 6017); São Francisco de Paula (MCN 29200, MCP 9837); São Leopoldo (MZSP 4721); Tenente Portela (MCP 10205); Viamão (MCP 5806, 4732, 5834, 5928, 4709, 8449); Xangrilá, Capão Canoa [?] (MCN 12070). URUGUAY *Artigas*: Arroio Duas Cruzes (MCN 18537). *Lavalleja*: Cerro Arequita, Arequita (IBSP). *Maldonado*: Piriapolis (CAS). *Treinta y Tres*: Rio Olmar Chico, 25 km WSW Treinta y Tres (AMNH). PARAGUAY Transchaco, km 470, Laguna Negro (IRSNB); km 640, La Medlon (IRSNB); Asunción (IBSP, MLP 13509). BOLIVIA *Pando*: San Borja, near Río Maniqui, Estac. Biolog. (SMNK 1291, 1330). *Cochabamba*: Cochabamba (CAS). *La Paz*: El Chiquimeni, Poço Petroleiro, Sapecho (MCN 24080); Yungas, Mapiri (AMNH); Apolol (AMNH). ARGENTINA *Misiones*: Cataratas del Iguazú (CAS, MACN); San Ignacio (MLP 13992); Santa María (MACN); Posadas (MACN); Puerto Bemberg (MACN). *Catamarca*: Catamarca (MACN). *Salta*: P. N. El Rey (MACN). *Corrientes*: Mercedes (MLP 16473). *Formosa*: Formosa, Arroyo Guaycolec (USNM). *Salta*: Santa Inapia (MACN); Rosari (ZMK); 8.4 km S Cafayate, 1,660 m (AMNH); El Rey Natl. Pk. 950 m (AMNH). *Chaco*: Formosa (MACN). *Santiago del Estero*: Termas de Río Hondo (AMNH). *Entre Ríos*: Entre Ríos (MACN); Salto Grande (MACN); Rosario de la Frontera (ZMK); Entre Ríos (MLP 13556); Villa Federal (MLP 13973); Reserva Mocoretá (MACN); Gualeguay (MACN); La Paz (MACN); San José (MACN). *Santa Fé*: Las Gamas, 20 km W Vera (MACN); Tostado (MACN). *Córdoba*: Valle Hermoso, 800 m (AMNH); La Falda [?] (MACN); Leones, many coll. (MACN); Calamuchita (MCN). *Buenos Aires*: Buenos Aires, many coll. (MACN); Colastiné (MLP); Moreno (MACN); Buenos Aires (CAS); San Isidro (MACN); Hurlingham (MACN); Sierra de la Ventana (MACN); Del Viso (MCN); Ascension (MCN); Florida (MACN); San Isidro (MACN); Tortugas (MACN); Lanos (MACN); Zelaya, many coll. (MACN); Punta Lara (MACN). *Río Negro*: Cororel Gómes, Nov. 1945, ♂ (I. Grasso, MLP); General Roca, Balsa C, Dec. 1962, ♀ (A. Bachmann, MACN). *La Pampa*: Santa Rosa, Dec. 1966, ♀ (MACN). *Chubut*: Puerto Madryn, ♀ (M. Doello, MCN). CHILE *Tarapacá*: Arica, 5 Apr. 1976, ♀ (N. Hichins, AMNH); Lluta River Valley nr. Arica, ♀ (G. Mann, AMNH); Pocon, 27 Jan. 1978, ♀♂ (W. Sedgwick, MCZ); Azapa, Jan. 1978, ♂ (W. Sedgwick, MCZ). *Antofagasta*: Caleta del Cobre, Taltal, 30, 31 Apr. 1959, ♀ (R. Wagenknecht, AMNH).

Argiope blanda O. P.-Cambridge
Map 2D; Figures 46–54

Argiope blanda O. P.-Cambridge, 1898: 267, pl. 37, fig. 2, ♂. Male holotype from Santa Ana, 20 km SW Cobán, Guatemala, in BMNH. Levi, 1968: 348, figs. 137–153, ♀♂. Platnick, 2003.

Diagnosis. The female differs from *A. argentata* in ventral coloration of the abdomen. The transverse band is as wide as the length of the anterior median black trapezoid (Fig. 49); there do not seem to be distinct differences from the epigynum of *A. argentata*, but the hole in the epigynum depression is round (Fig. 48).

The palpus of the male differs from all other species by having a large cone at the base of the embolus (arrow, Fig. 53; Fig. 54).

Variation. Total length of females 9.0–

14.5 mm, males 2.7–4.3 mm. The size of the round opening inside the epigynum depression varies. The illustrations (Figs. 46–48, 53, 54) were made from specimens from Costa Rica.

Distribution. Southern Texas to Costa Rica (Map 2D).

Additional Records. UNITED STATES, TEXAS *Cameron Co.*: Sabal Palm Grove, ca. 6.4 km SE Brownsville, 31 May 1983, 1♂ (W. Maddison, MCZ). MEXICO *San Luis Potosí*: 13 km W San Joaquin, 21°45′N, 88°57′W, 19 Apr. l963, 1♂ (W. J. Gertsch, W. Ivie, AMNH); Rt. 120, NE Xilitla, 27 May 1982, 1♀ (F. Coyle, MCZ). *Veracruz*: Catemaco, 95°4′W, 18°25′N, 9 Aug. 1966, 1♀ (J., W. Ivie, AMNH); 4 Sep. 1968, ♀ (A. F. Archer, AMNH). *Chiapas*: 8 km NE Huixtla, 1 Sep. 1980, 1♀ (E. S. Ross, CAS); Chiapas, 1920, 1 imm. (L. Hotzen, USNM). COSTA RICA *Guanacaste*: Palo Verde Biol. Station, 25 km SSW Bagaces, 16–22 Jan. 1978, 1♂ (W. Eberhard, MCZ). *Puntarenas*: Osa Peninsula, 4 km SW Rincon, Mar. 1967, 1♀ (OTS course, MCZ). *San José*: San José, ca. 1945, 1♂ (E. Schmidt, AMNH).

Argiope savignyi Levi
Map 2B; Figures 55–63

Argiope savignyi Levi, 1968: 350, figs. 154–169, ♀♂. Male holotype from Barro Colorado Island, Lago Gatun, Panama in the MCZ. Platnick, 2003.

Diagnosis. The female differs from all others by the coloration of the abdomen dorsally, the posterior being black, containing few white spots (Fig. 59), ventrally by the broken transverse line, each half angled anteriorly (Fig. 58). The epigynum differs by having the posterior portion larger; posteriorly the septum is more massive (Figs. 55, 56).

Males of *A. savignyi* differ from *A. argentata* by lacking the spur near the embolus tip (Fig. 63), and from *A. blanda* by lacking the cone at the base of the embolus (Figs. 62, 63) and by having the hematodocha within the embolus coil (Fig. 63) and the base of the embolus slightly different in shape (Fig. 62).

Variation. Total length of females 12.7–18 mm, males 3.2–4.7 mm. The septum of the epigynum is quite variable in width and length (Levi, 1968). All illustrations were made from specimens from the former Canal Zone [now Panamá Prov.], Panama.

Natural History. In seasonal forest and roadside bushes in Yucatan.

Distribution. From Yucatan, Mexico, to southern Brazil (Map 2B).

Additional Records. MEXICO *Yucatan*: 3 km E Chichen Itza ruins on Hwy. 180, 19–20 July 1983, 1♂ (W. Maddison, R. S. Anderson, MCZ); Balankanche Cave 2 km E of Chichen Itza, 19 July 1983, 1♂ (W. Maddison, MCZ). NICARAGUA Escondida River, 80 km from Bluefields, 25 Oct. 1892, 1♀ (C. W. Richmond, USNM). COSTA RICA *Heredia*: Puerto Viejo de Sarapiqui, La Selva, 50 m, 12 Jan. 1986, 1♀ (J. Coddington, USNM). *Puntarenas*: Golfita, 3–8 July 1957, 1♀ (F. S. Truxal, AMNH). PANAMA *Panamá*: Forest Reserve [Soberiana Natl. Park], 23 July 1950, 1♀, 1♂ (A. M. Chickering, MCZ); Pipeline Road [Soberiana Natl. Park], 6 Jan. 1977, 1♀ (H. Levi, M. Robinson, MCZ); Barro Colorado Island, 13 Jan. 1968, 1♀ (M. Robinson, MCZ); Carti Road, 8 km NNW El Llano, 400 m, 4 Aug. 1983, ♀ (H. Stockwell, MCZ); Cerro Galero, July 1985, ♂ (W. Eberhard, MCZ). SURINAME *Brokopondo*: Brownsberg Reserve, 4°50′N, 55°15′W, May 1984, ♀ (D. Smith, MCZ). COLOMBIA *Santander*: Río Suarez, 800–1,000 m, 11–17 Aug. 1946, ♀ (AMNH). *Antioquia*: Mutatá, Dec. 1963, 1♀ (P. B. Schneble, MCZ). *Meta*: Puerto Lleras, Lomalinda, 3°18′N, 73°22′W, Sep. 1987, 1♀ (B. T. Carroll, CAS). *Choco/Putumayo*: S Quibdo, Río Atrata, 19 July 1983 (Coyle, AMNH); road from Puerto Lima to Santa Lucia, 240 m, 1 Jan. l973, 3♀ (Leist, SMNK 3059a). *Valle*: Baja Calima nr. Puerto Patiña, 10–13 July 1981, 1♂ (B. Opell, MCZ). ECUADOR Quevedo, 20 Apr. 1976, 1♀ (Fritz, MACN) *Pichincha*: Tinalandia, nr. Santo Domingo de las Colorados, 7 Dec. 1981 (E. Schlinger, CAS). *Napo*: 20 km E Puerto Napo, Alinahuí, 1°0′S, 77°25′W, Nov.–Dec. 1995, 1♀ (E. S. Ross, CAS); Limoncocha, 240 m, 6 Feb. 1979, 1♀ (L. Burnham, MCZ); 20 km E. Puerto Napo, Alinahuí, 1°0′S, 77°25′W (E. S. Ross, CAS). PERU *Huanuco*: Huallaga Vall., Cucharas, Feb.–Apr. 1954, 1♀ (F. Woytkowski, CAS). *Madre de Dios*: Reservada Tambobata, 31 Oct.–6 Nov.1986, 1♀ (A. Rypstra, USNM); Zona Reservada de Manu, Puesto de Vigil. Pakitza, 11°58′S, 71°18′W, 4 Oct. l987, 1♀ (D. Silva, J. Coddington, USNM). BRAZIL *Bahia*: Fazenda Jacarandá, Itamarajú, 9 Dec. 1977, 1♀ (J. S. Santos, MCN 11028); Fazenda Nosso Senhora das Neves, Itamarajú, 9 Oct. 1978, 1♂ (J. S. Santos, MCN 11020). *Espírito Santa*: Linares, 31 Aug. 1966, imm. (H. Reichardt, 5308a). *Mato Grosso*: Sinop, 1976, 1♀ (O. Roppa, AMNH). *São Paulo*: Res. Ecol. Juréia-Itatins, Iguape, 19 Feb. 1996, 1♀ (R. S. Bérnils, MZSP 15514).

Argiope ericae new species
Map 2C; Figures 64–73

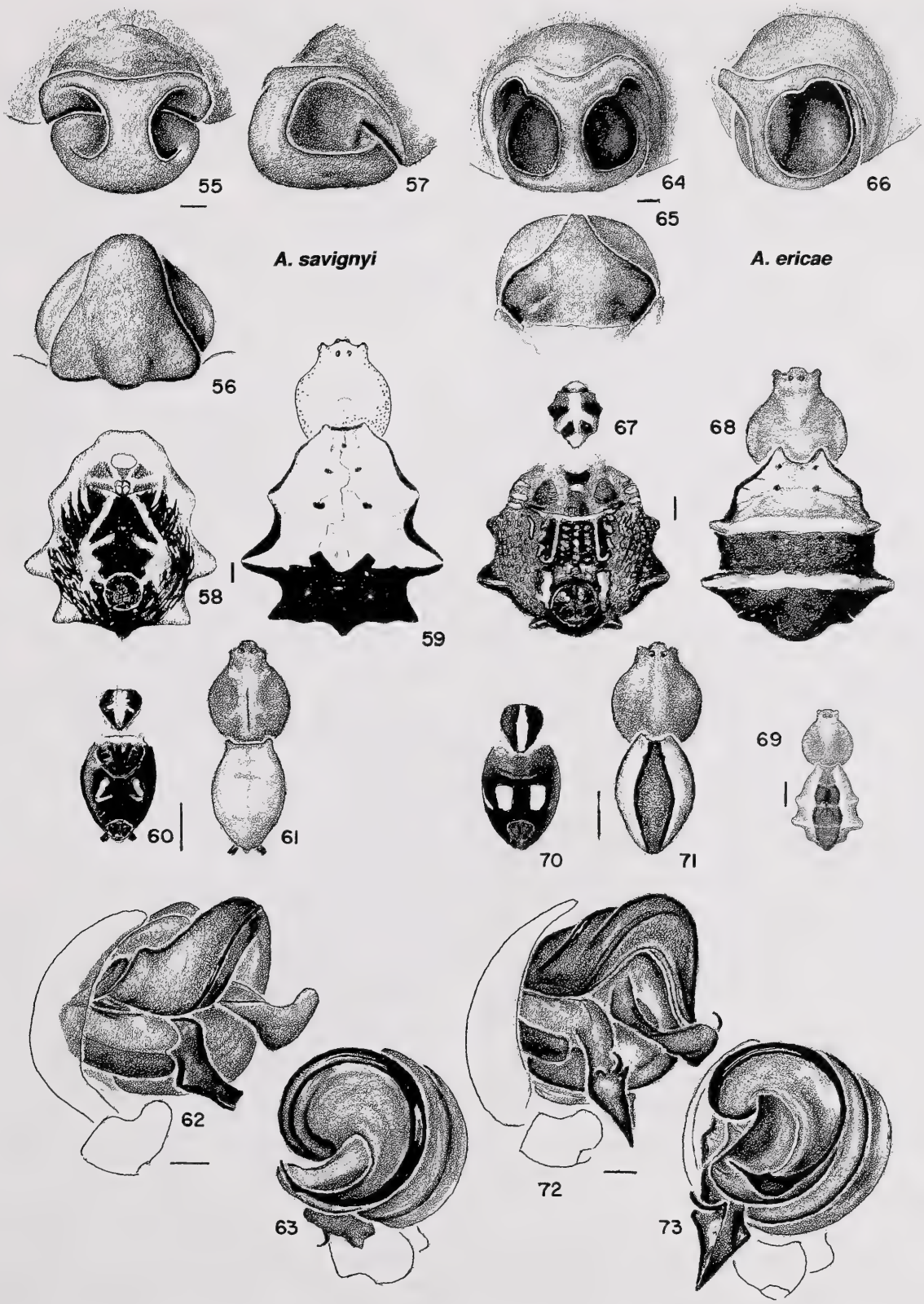
Holotype. Male holotype from Garruchos, São Borja, Rio Grande do Sul, Brazil, 6 Dec. 1975 (A. Lise, MCN 3181). The species is named after Erica Helena Buckup, arachnologist and helpful curator of the MCN collection.

Description. Female allotype. Carapace, brown, lighter in median longitudinal area, eye region darker (Fig. 68). Chelicerae brown, distally light yellowish. Endites, labium dark brown, distally light. Sternum black with median, longitudinal white band having a pair of posteriorly directed branches (Fig. 67). Legs black with yellow rings almost as wide as black areas, more distinct ventrally. Abdomen with two dorsal black transverse bands and a gray one anteriorly, and a dusky spot between anterior tubercles (Fig. 68). Venter black, with a pair of thin white longitudinal lines, a narrow transverse line behind epigynum and on sides of spinnerets a large white patch; numerous white spots on sides and between white lines (Fig. 67). Anterior lateral eyes 0.6 diameters of anterior medians, posterior median eyes 1.0, posterior lateral eyes 1.2 diameters. Anterior medians 1.2 diameters apart, posterior medians 1.5 diameters apart. Lateral eyes on a tubercle, anterior eye facing ventrally and forward, posterior eye facing ventrally and half forward and to the side. Abdomen anteriorly with a pair of small projections, and three pairs of lateral humps, the third very small (Fig. 68). Total length 13 mm. Carapace 5.2 mm long, 4.8 wide in thoracic region, 2.2 wide in cephalic region. First femur 8.0 mm, patella and tibia 9.2, metatarsus 8.7, tarsus 2.1. Second patella and tibia 8.0 mm, third 5.2. Fourth femur 9.1 mm, patella and tibia 8.0, metatarsus 7.7, tarsus 2.2.

Male holotype. Carapace, chelicerae, endites, labium colored as in female (Fig. 71). Sternum dark brown with median, longitudinal white band. Legs dark brown, not banded. Abdomen with dorsal, median, longitudinal nearly black band with white on each side (Fig. 71); venter with a pair of white spots on black, and laterally a diagonal white line (Fig. 70). Anterior lateral eyes 0.8 diameters of anterior medians, posterior median eyes 1.2, posterior lateral eyes 1 diameter. Anterior medians 1.3 diameters apart, 1.3 from laterals. Posterior medians 1.5 diameters apart, 1.6 from laterals. Abdomen oval, pointed behind and anteriorly with a pair of small projections (Fig. 71). Total length 4.6 mm. Carapace 2.3 mm long, 2.0 wide in thoracic region, 0.8 wide behind posterior lateral eyes. First femur 3.2 mm, patella and tibia 3.4, metatarsus 2.8, tarsus 1.2. Second patella and tibia 3.3 mm, third 1.7, fourth 2.7.

Variation. Total length of females 13.0–16.5 mm, males 4.8–5.6 mm. The penultimate female has dorsal transverse bands as in the adults, the black venter has a pair of exclamation point marks, the dots whiter than the line above. The dots are anteriorly lateral to spinnerets, apparently derived from the pair of white ventral spots of the immature. A younger female shows the dorsal longitudinal abdominal white band of early instars, changing into transverse bands (Fig. 69). The male paratypes have the conductor straighter than the curled one of the illustrated male holotype (Figs. 72, 73).

Diagnosis. No other American species is marked as is *A. ericae* (Figs. 67, 68, 70, 71). The absence of the white, transverse, ventral band separates *A. ericae* from *A. argentata.* The epigynum has a distinct tubercle on the anterior lip of the opening (Figs. 64, 66). The third and fourth femora are slightly longer than their respective tibiae. The male markings, a dorsal, longitudinal, dark band on the abdomen (Fig. 71) and a pair of ventral white patches (Fig. 70) separate *A. ericae* from all other American species. The median apophysis of the palpus is distally pointed (at 5h in Fig. 72, at 7h in Fig. 73) and the tip of the embolus has a distinct shape (Fig. 73).



Figures 55–63, *Argiope savignyi* Levi. 55–59, female. 55–57, epigynum. 55, ventral. 56, posterior. 57, lateral, 58, abdomen, ventral. 59, dorsal. 60–63, male. 60, sternum and abdomen, ventral. 61, dorsal. 62, 63, left palpus. 62, mesal. 63, ventral.

Figures 64–73, *Argiope ericae,* new species. 64–69, female. 64–66, epigynum. 64, ventral. 65, posterior. 66, lateral, 67, abdomen, ventral. 68, dorsal. 69, immature, dorsal. 70–73, male. 70, sternum and abdomen, ventral. 71, dorsal. 72, 73, palpus. 72, mesal. 73, ventral.

Scale lines, 1.0 mm, genitalia, 0.1 mm.

Distribution. São Paulo State, Brazil, to northeastern Argentina (Map 2C).

Paratypes. BRAZIL *Rio Grande do Sul*: Garruchos, S Borja, 7 Dec. 1975, 1♂ (A. Lise, MCN 3197). ARGENTINA *Misiones*: Iguazú, 1♂ (Prosen, MLP); Río Urugua-í, Pto. Bemberg [Pto. Libertad], 1 Feb. 1950, penult. ♀ (Giai-Partridge, MACN 3161); San Antonio, 2 Mar. 1951, ♀ (W. Partridge, MACN 3410). *Entre Ríos*: Parque Nacional El Palmar, Feb. 1981, ♀ allotype (P. Goloboff, MACN).

Specimens Examined. BRAZIL *São Paulo*: São Roque, 14 June 1959, 1 imm., 1♂ (F. Lane, AMNH). *Paraná*: Ponte do Rio Coutinho, Guarapuava, 28 Apr.1967, 1 imm. (P. de Biasi, MZSP 6990). *Rio Grande do Sul*: Porteira Sete, Cachoeira do Sul, 31 Oct. 1992, 1 imm. ♂ (R. G. Buss, MCP 3423); Capão de Padre Reus, São Leopoldo, 27 Aug. 1966, 1 imm. (MZSP 5506). ARGENTINA *Misiones*: Eldorado, 26°28′S, 54°43′W, 1 Sep.–15 Nov. 1964, 3 imm. (A. Kovacs, AMNH).

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Systematics of Snakes of the *Dipsas oreas* Complex (Colubridae: Dipsadinae) in Western Ecuador and Peru, with Revalidation of *D. elegans* (Boulenger) and *D. ellipsifera* (Boulenger)

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SYSTEMATICS OF SNAKES OF THE *DIPSAS OREAS* COMPLEX (COLUBRIDAE: DIPSADINAE) IN WESTERN ECUADOR AND PERU, WITH REVALIDATION OF *D. ELEGANS* (BOULENGER) AND *D. ELLIPSIFERA* (BOULENGER)

JOHN E. CADLE[1]

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ABSTRACT. The systematics and biology of colubrid snakes from western Ecuador and northern Peru in the *Dipsas oreas* group, comprising the nominal taxa *D. oreas* (Cope), *D. elegans* (Boulenger), and *D. ellipsifera* (Boulenger), are reviewed. The last two species are resurrected from the synonymy of *D. oreas.* These species, especially *D. elegans* and *D. ellipsifera,* have been confused in previous literature because of inadequate attention to patterns of sexual dimorphism and geographic variation. *Dipsas elegans* and *D. ellipsifera* share a distinctive color pattern that is quite different from color patterns in *D. oreas. Dipsas ellipsifera* differs from both *D. oreas* and *D. elegans* in having lower ventral and subcaudal counts, but sexes must be analyzed separately to see the distinctions clearly. Other subtle characters of scutellation, coloration, and dentition aid in distinguishing these species. *Dipsas elegans* is unusual in that males have significantly more ventral scutes than females, the reverse of the more common colubrid pattern of sexual dimorphism, in which females have more ventrals than males; neither *D. oreas* nor *D. ellipsifera* is sexually dimorphic for this character.

Dipsas ellipsifera is known only from the valley of the Río Mira in extreme northwestern Ecuador (Imababura Province). *Dipsas elegans* is known from the western versant of the Andes in Ecuador from just north of the equator to about latitude 2°S; it is also found in the inter-Andean valley of the upper Río Guayllabamba east of Quito. *Dipsas oreas* is known from southern Chimborazo and Guayas Provinces south to Loja Province in southern Ecuador, thence south along the western slopes of the Andes to at least the Río Zaña (6°51′S) in northern Peru. The occurrence and distribution of *D. oreas* in Peru is detailed for the first time. Most localities for *D. oreas* are on the Andean slopes, but the species is also recorded by specimens from the lowlands in the vicinity of Guayaquil, Ecuador. The type locality of *D. oreas* and many other South American amphibians and reptiles obtained by the naturalist James Orton is the "elevated Valley of Quito," which has been errone-

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ously interpreted narrowly as the vicinity of Quito, Ecuador. Orton's own writings show that a broader interpretation encompassing virtually all of the Ecuadorian highlands was intended. The ranges of *D. elegans, D. ellipsifera,* and *D. oreas* are very likely extremely fragmented because of significant destruction of forest habitats in western Ecuador and Peru.

Hemipenes of *Dipsas elegans, D. ellipsifera,* and *D. oreas* are slightly bilobed, fully capitate, and have ornamentation similar to other species of the tribe Dipsadini (*Dipsas, Sibon, Sibynomorphus,* and *Tropidodipsas*). The capitulum is ornamented with papillate calyces and the sulcus spermaticus bifurcates within the capitulum. Proximal to the capitulum a battery of enlarged spines encircles the midsection of the organ. A large basal nude pocket is present on the hemipenis in all three species.

Notes on coloration, natural history, and behavior are reported for the three species of the *oreas* group, although most observations are for *Dipsas oreas.* In northern Peru, *D. oreas* shows extensive intrapopulational variation in coloration, which could in part be sexually dimorphic. It is unclear whether this variation pertains to other parts of the distribution. *Dipsas oreas* is active nocturnally in low vegetation but seeks seclusion in leaf litter or under surface objects on the ground during the day. This diel behavior pattern is also reported for several other species of *Dipsas* and might be common in the genus. In northern Peru, the activity of adult *D. oreas* is strongly seasonal and coincides with the rainy season. A peculiar aggregation of *Dipsas oreas* encountered at a locality in northern Peru is described. Comprising one female and six males, this is the first reported case of "aggregation behavior" in any snake of the tribe Dipsadini and one of very few observations of such behavior in Neotropical colubrids. Details of the aggregation suggest an association with mating, and the existence of communal nesting in this species suggests that aggregation might occur for oviposition as well.

A key to all species of *Dipsas* reported or expected in western South America (Colombia, Ecuador, and Peru) is provided. This includes six species known from western Ecuador (*andiana, elegans, ellipsifera, gracilis, oreas,* and *temporalis*), two of which (*gracilis, oreas*) also occur in western Peru, and three additional species known or expected in Chocoan Colombia (*nicholsi, sanctijohannis,* and *viguieri*). *Dipsas gracilis* and *D. viguieri* are not distinguishable by any reported characteristics of the taxa. Brief notes are provided on the occurrence of *D. gracilis* in northwestern Peru. Some taxonomic issues concerning two species of the Amazonian versant, *D. latifasciata* and *D. latifrontalis,* are outlined. These species are not clearly distinguishable on the basis of characters discussed in the literature, and the assignment of these names to specimens from eastern Ecuador needs to be reviewed in conjunction with study of their holotypes.

RESUMEN. Se revisan la sistemática y biología de las serpientes de la familia Colubridae de Ecuador occidental y el norte del Perú en el grupo *Dipsas oreas,* que se compone de los taxones nominales *D. oreas* (Cope), *D. elegans* (Boulenger), y *D. ellipsifera* (Boulenger). Las últimas dos especies se resucitan de la sinonimia de *D. oreas.* Estas especies, especialmente *D. elegans* y *D. ellipsifera,* se confusaron en la literatura anterior debido a insuficiente atención a los patrones de dimorfismo sexual y la variación geográfica. *Dipsas elegans* y *D. ellipsifera* comparten un patron de colores bien distinto y substantivamente diferente de los patrones en *D. oreas. Dipsas ellipsifera* es distinto de *D. oreas* y *D. elegans* al tener bajos cuentos de ventrales y subcaudales, pero es necesario analizar por separado los sexos para ver claramente las distinciones. Otros carácteres más sutil de la escamación, la coloración, y la dentición ayudan al distinguir estas especies. *Dipsas elegans* es extraño ya que los machos tienen considerablemente más escamas ventrales que las hembras, lo contrario del patrón común de dimorfismo sexual en la familia Colubridae, en que las hembras tienen más ventrales que los machos; ni *D. oreas* ni *D. ellipsifera* demuestra dimorfismo sexual en esta carácter.

Dipsas ellipsifera se conoce solamente del valle del Río Mira al norte extremo del Ecuador (Provincia de Imbabura). *Dipsas elegans* se conoce del lado occidental de los Andes en Ecuador desde justo al norte del ecuador hasta aproximadamente la latitud 2°S; se encuenta también en el valle interandino del alto Río Guayllabamba al este de Quito. *Dipsas oreas* se conoce desde la parte sur de las provincias Chimborazo y Guayas hasta la provincia Loja en el sur de Ecuador, desde allí a lo largo de las vertientes occidentales de los Andes, por lo menos hasta el Río Zaña (6°51′S) en el norte de Perú. La presencia y distribución de *D. oreas* en Perú se detallan para la primera vez. La mayoría de las localidades para *D. oreas* se encuentra en las vertientes Andinas, pero también es recordado por ejemplares de tierras bajas vecino a Guayaquil, Ecuador. La localidad típica de *D. oreas* y muchas otras especies de anfibios y reptiles sudamericanos que fueron obtenido por la naturalista James Orton es "el valle elevado de Quito", que se han interpretado estrechamente y equivocadamente como los alrededores de la ciudad de Quito, Ecuador. Las obras propias de Orton demuestran que el quisó decir una interpretación más amplia, que abarcó casi todas las partes altoandinas Ecuadorianas. Los rangos de *D. elegans, D. ellipsifera,* y *D. oreas* son probablemente muy fragmentados debido a la destrucción substantiva de los bosques en Ecuador y Perú occidental.

Los hemipenes de *Dipsas elegans, D. ellipsifera,* y *D. oreas* son ligeramente bilobulados, completamente capitatos, y tienen ornamentación similar a otras especies del tribo Dipsadini (*Dipsas, Sibon, Sibynomorphus,* y *Tropidodipsas*). El capítulo es ornamentado con cálices que llevan papilas, y el surco espermático se divide dentro del capítulo. Proximal al capítulo hay una serie de espinas agrandadas que rodean

el órgano. Un bolsillo desnudo y grande se encuentra en la base del hemipene de las tres especies.

Se reportan notas sobre la coloración, la historia natural, y el comportamiento para las tres especies del grupo *oreas*, aunque la mayoría de las observaciones son para *Dipsas oreas*. En el norte de Perú, *D. oreas* muestra mucha variación intrapoblacional en colores. En parte, esta podria ser debido al dimorfismo sexual. No es claro si esta variación pertenece a otras partes de su distribución. *Dipsas oreas* es activo nocturnamente en vegetación baja, pero por día se encuentra en la hojarasca o debajo de objetos sobre la superficie de la tierra. Este patron de comportamiento diario se reporta para varias otras especies de *Dipsas* y puede ser común en el género. En el norte del Perú, la actividad de adultos de *D. oreas* es muy estacional y corresponde fuertamente con la época de lluvias. Se describe una agregación extraña de *Dipsas oreas* que se halló en una localidad de campo en el norte del Perú. Compuesto de una hembra y seis machos, esto es el primero reporte de "comportamiento de agregación" en una especie del tribo Dipsadini y es uno de muy pocas observaciones de tal comportamiento en colubrideos Neotropicales. Los detalles sugeren que la agregación fue asociada con el acoplamiento y la existencia de nidos comunales en esta especie sugere que agregación puede suceder también por poner huevos.

Se provee una clave para todas las especies de *Dipsas* conocidas o esperadas en Sudamérica occidental (Colombia, Ecuador, Perú). Estas incluyen seis especies conocidas del Ecuador occidental (*andiana, elegans, ellipsifera, gracilis, oreas, temporalis*), de las cuales dos (*gracilis, oreas*) también se encuentran en el Perú occidental; se conocen o se esperan tres especies adicionales en el Chocó de Colombia (*nicholsi, sanctijohannis, viguieri*). No se pueden distinguir *D. gracilis* y *D. viguieri* por las características reportadas en la literatura. Se proveen notas breves sobre la presencia de *D. gracilis* en el noroeste del Perú. Se resumen algunos problemas acerca de la taxonomía de dos especies de la vertiente amazónica, *D. latifasciata* y *D. latifrontalis*. No se pueden distinguir estas especies por las características en la literatura, y es necesario revisar el uso de estos nombres para especimenes desde Ecuador oriental conjunto con estudio de los holotipos.

INTRODUCTION

Neotropical snakes of the genus *Dipsas* (Colubridae: Dipsadinae: Dipsadini) were last comprehensively reviewed by Peters (1960a). Many South American species remain poorly known because they are represented by few specimens and/or they exhibit complex variation in characters, such as color pattern and scutellation, typically used to infer species limits in snakes. Several species in western Ecuador and Peru have been poorly characterized in existing literature, making species determinations of certain populations difficult. At the time that Peters (1960a) and Peters and Orejas-Miranda (1970) reviewed *Dipsas*, a few species were known from western Ecuador, but none was recorded from the western slopes of the Andes or Pacific lowlands in Peru. The availability of new material makes review of these species timely because of the confused state of the systematics of several species in western Ecuador and misapplied names to many specimens already in collections. A subsequent paper (Cadle, unpublished data) will review new material of the related genus *Sibynomorphus*.

Peters (1960a) and Peters and Orejas-Miranda (1970) thought that three species groups of *Dipsas* were represented in western Ecuador: (1) the *variegata* group, represented in western Ecuador by *D. variegata variegata* and *D. variegata nicholsi*; (2) the *oreas* group, represented by *D. oreas, D. ellipsifera,* and, as clarified later by Kofron (1982), *D. elegans*; and (3) the *articulata* group, represented in western Ecuador by *D. gracilis* and *D. temporalis*. Subsequent to Kofron's (1982) review, *D. elegans* and *D. ellipsifera* were recognized as subspecies of *D. oreas* (Orcés and Almendáriz, 1987). Until recently, none of these species was known from Peru, but Cadle and Chuna (1995) and Tello (1998) reported *D. oreas* and *D. gracilis*, respectively, from northern Peru. Species in the *variegata* and *oreas* groups, in particular, have presented complex systematic problems, resulting in numerous misidentified specimens (e.g., several unrelated species confused with *D. variegata*; Cadle and Myers, 2003). Consequently, several species within these groups from Ecuador and Peru have routinely been confused, prompting me to review these groups while identifying collections resulting from biological inventories in northern Peru.

Cadle and Myers (2003) reviewed the

"*Dipsas variegata*" group (*sensu* Peters, 1960a) in Panama and western South America. Their principal conclusions relevant to the identity of species of *Dipsas* in western Ecuador were (1) specimens from Ecuador previously referred to *Dipsas v. variegata* were misidentified specimens of *D. oreas, D. andiana,* or *Sibynomorphus petersi,* all of which are well known from western Ecuador, and (2) Ecuadorian specimens identified as *D. v. nicholsi* by Peters (1960a) are a distinct species, *Dipsas andiana* (Boulenger), a name resurrected from the synonymy of *D. oreas,* where it had been placed by Peters (1960a). Thus, no definitive records of *Dipsas variegata* are known from Panama, Colombia, Ecuador, or Peru, and the close relationship of *D. andiana* to *D. variegata* seems highly questionable. See Cadle and Myers (2003) for further details.

Cadle and Myers (2003) briefly characterized *Dipsas oreas* in diagnosing *D. andiana.* They examined specimens of the nominal taxa *elegans* and *ellipsifera* but left their relationship to *D. oreas* as an "open question" (Cadle and Myers, 2003: footnote 13). This paper extends their discussion of *Dipsas oreas* and evaluates the status of *D. elegans* and *D. ellipsifera.* In addition, I summarize natural history and behavioral observations for these species and provide a key for the identification of all species of *Dipsas* known or expected from west of the Andes in Colombia, Ecuador, and Peru.

METHODS

Localities: The Río Zaña Study Site. Most of my observations on the natural history of *Dipsas oreas* in Peru are derived from field work conducted in the vicinity of Monte Seco (also known as Monteseco), a small town on the north side of the Río Zaña in western Cajamarca department, Peru (6°51′S, 79°6′W). Thus, it seems pertinent to make a few brief comments on this locality and others in northern Peru where *D. oreas* is known to occur.

In 1987 (early dry season: May–June) and 1989 (early rainy season: January) for a combined total of 11 weeks, I made herpetological collections in the Monte Seco region; some results from those surveys were reported previously (Cadle, 1989, 1991; Cadle and Chuna, 1995; Cadle and McDiarmid, 1990). In the late 1980s and early 1990s, humid montane forest covered the Andean slopes above Monte Seco from approximately 1,500 to 2,500 m, with an areal extent estimated to be 2,500 ha (Sagástegui et al., "2003" [2004]). Above 2,500 m in the immediate vicinity were tablelands and slopes that had been largely cleared of forests, although forest fragments still existed up to nearly 3,000 m. Specific survey sites at Monte Seco varied, and fieldwork sampled a wide elevation range concentrated between 1,200 and 2,500 m; less intense sampling was conducted down to 1,000 m and as high as 3,000 m. The primary focus of the field work was dense humid montane forest covering the mountain slopes, but other habitats, including agricultural land (coffee plantations, secondary forests) and open highland grasslands and bushlands, were also sampled. The known flora of Bosque Monte Seco comprises approximately 380 species of flowering plants and 40 species of pteridophytes (Sagástegui et al., 2004).

Wet and dry seasons at the Río Zaña Study Site are very pronounced, with a distinct rainy season occurring from approximately December to April. Temperatures recorded using a maximum/minimum mercury thermometer at the base camp (1,800 m) were as follows:

5 May–26 June 1987 (50 days, early dry season)
Maximum daily average, 28.5° C
(range 21.5°–35.5° C)
Minimum daily average, 9.2° C
(range 5.5°–12° C)

14–29 January 1991 (12 days, early rainy season)
Maximum daily average, 19.5° C
(range 16.5°–21° C)

Minimum daily average, 10.7° C
(range 10°–12° C)

The difference between the dry and rainy season maximum daily temperatures at the study site is because many days during the rainy season are prone to dense fog or cloud cover, whereas fog is rare during the dry season. These records show that the minimum daily temperature range was much greater during the dry season (characterized by clear, cool evenings) than during the rainy season (foggy/cloudy, warmer evenings), even though average minimum temperatures are similar.

Cadle (1989, 1991), Cadle and Chuna (1995), and Cadle and McDiarmid (1990) give additional details on the geography and habitats of the Monte Seco region. Dillon et al. (1995) included the humid forest of Monte Seco in a floristic study of western Peru and Ecuador, Sagástegui and Dillon (1991) provided a checklist of its flora, and Sagástegui et al. (2004) included the site in a comparative floral analysis of humid montane forests of northern Peru. For simplicity, in this paper I refer to all specific localities within the Monte Seco area as the Río Zaña Study Site and give elevation and habitat detail where pertinent. Descriptions or photographs of the Río Zaña Study Site and some other localities cited herein are given by Cadle (1991), Cadle and Chuna (1995), and Sagástegui et al. (2004). The herpetological collections made at the Río Zaña Study Site in 1987 and 1990 were timely, inasmuch as a considerable portion of the humid forest was cut and burned in the mid-1990s to provide pasturage for cattle and land for coffee production (see Sagástegui et al., 2004: figs. 6, 7). The site should be resurveyed to determine how much of its unique herpetofauna survives and to provide a baseline for its future recovery or extinction.

Elevations for my field sites were determined with a Thommen© altimeter, usually in conjunction with topographic maps. Coordinates and elevations for other localities, unless given by the collectors or otherwise stated, were derived from ornithological gazetteers of the Neotropics (Paynter, 1993, 1997; Stephens and Traylor, 1983); from Peruvian departmental maps or 1:50,000 topographic maps produced by the Instituto Geográfico Nacional, Lima; or from the online versions of the gazetteers of the U.S. Board on Geographic Names at the GEOnet© names server (http://earth-info.nga.mil/gns/html/index.html; the Web address seems to change with great frequency but should be searchable with the name GEONET). Bracketed data in localities are inferences from these sources. Abbreviations for museums in which cited specimens are housed are given in the list of specimens examined.

Systematic Characters, with Special Reference to Dipsas. I followed standard methods used in previous studies of snake systematics (e.g., Cadle, 1996; Cadle and Myers, 2003; Myers, 1974). Because some scutellation characters are highly variable intraspecifically within *Dipsas,* I here comment on the nature of the variation and ways in which some of these characters were recorded.

Peters (1960a: 25) noted the extreme variability of head scale patterns within *Dipsas*: "Division, extra suturing, or fusion takes place in nearly every head scale in this genus." Scale patterns of the temporal region in *Dipsas* are especially prone to intraspecific variation (Peters, 1960a: 26; Cadle and Myers, 2003: table 1), and the patterns of fragmentation and fusion of temporal scales make concise character definitions of species difficult. Generally, I attempted only to score primary and secondary temporals, and even this proved difficult in some cases. A few other head scale patterns seem useful in distinguishing some species pairs, especially when the frequencies of alternative states are considered. In this category are scales in the loreal region involving the loreal, postnasals, preoculars, and prefrontals; a few comments concerning scale patterns in this area are warranted because they are help-

ful in distinguishing species considered herein.

In those cases in which only a single scale is present between the postnasal scale and the eye, I follow Peters (1960a: 7–8) in considering this scale to be a loreal. A preocular scale, when present in *Dipsas,* is small, usually located superior to the loreal, and bordered by the loreal, prefrontal, supraocular, and eye (Fig. 1). This terminology is also consistent with definitions given by Savage (1973), but *Dipsas* differs from the more common colubrid conditions commented upon by Savage. Savage (1973: fig. 1) considered the common condition in which the preocular scale separates the loreal scale from the anterior border of the eye (i.e., the preocular is intercalated entirely between the eye and loreal); Savage also considered patterns of scale fusions involving the loreal + prefrontal. In contrast, in *Dipsas* the preocular typically lies superior to the loreal (Fig. 1), and the loreal contacts the anterior border of the eye; scale fusions usually involve the preocular + prefrontal.

Differences among the species of *Dipsas* considered herein involved primarily two characters of the loreal region: (1) the shape of the loreal scale itself, which was either square/polygonal or much longer than tall (rectangular), and (2) whether a preocular appeared as a distinct scale (usually superior to the loreal) or was fused with the prefrontal scale (in which case the fused prefrontal–preocular touches the anterior border of the eye). Four patterns in scales of the loreal region were most frequent, loreal patterns 1–4 (Fig. 1), distinguished by the two characters of the loreal and preocular scales just mentioned. In addition to these common patterns, a few rarer conditions were observed, which involved either the presence of a subpreocular (formed by a suture segregating the posteroventral corner of the loreal from the main part of that scale; loreal pattern 5, Fig. 1) or horizontal partition of the loreal, nasals, and/or prefrontals to form an unusually long preocular above the loreal (loreal pattern 6, Fig. 1).

Loreal patterns 1 and 2 are identical except for the presence or absence of a discrete suture separating the preocular scale from the prefrontal scale. Patterns 3 and 4 are related in a similar way. Usually a single pattern overwhelmingly predominated for each species (see Tables 1 and 3 and the discussion of *Dipsas oreas* for exceptions). In all cases of intraspecific variability in patterns 1–4, alternative states within a species were always either Patterns 1 and 2 or patterns 3 and 4 (and never, e.g., pattern 1 with pattern 4). For example, in *D. oreas,* in which pattern 2 was overwhelmingly frequent, alternate states involved pattern 1 or other rare patterns, but never patterns 3 or 4. Patterns 5 and 6 appeared with less frequency than any other patterns, except for a high frequency of pattern 6 within one population of *D. oreas* (see below).

One reviewer of this paper suggested including total segmental counts (ventrals + subcaudals) as part of the diagnoses and descriptions of these species, and as a summary to aid in sexing of specimens (the idea being that total segmental counts would add together whatever smaller sexual dimorphism might exist within ventral or subcaudal counts considered separately, thus enhancing the distinction between sexes). This would perhaps permit easier sexing of specimens without the need for dissection. Although this approach seems useful for some groups of snakes, several aspects of variation within the snakes considered herein make the use of total segmental counts less useful, and exclusive consideration of total counts actually obscures some patterns apparent from consideration of ventral and subcaudal counts separately.

Two of the species considered herein (*Dipsas oreas* and *D. ellipsifera*) are not at all sexually dimorphic in ventral counts, but strongly dimorphic in subcaudal counts (male counts higher than female counts with virtually no overlap in counts

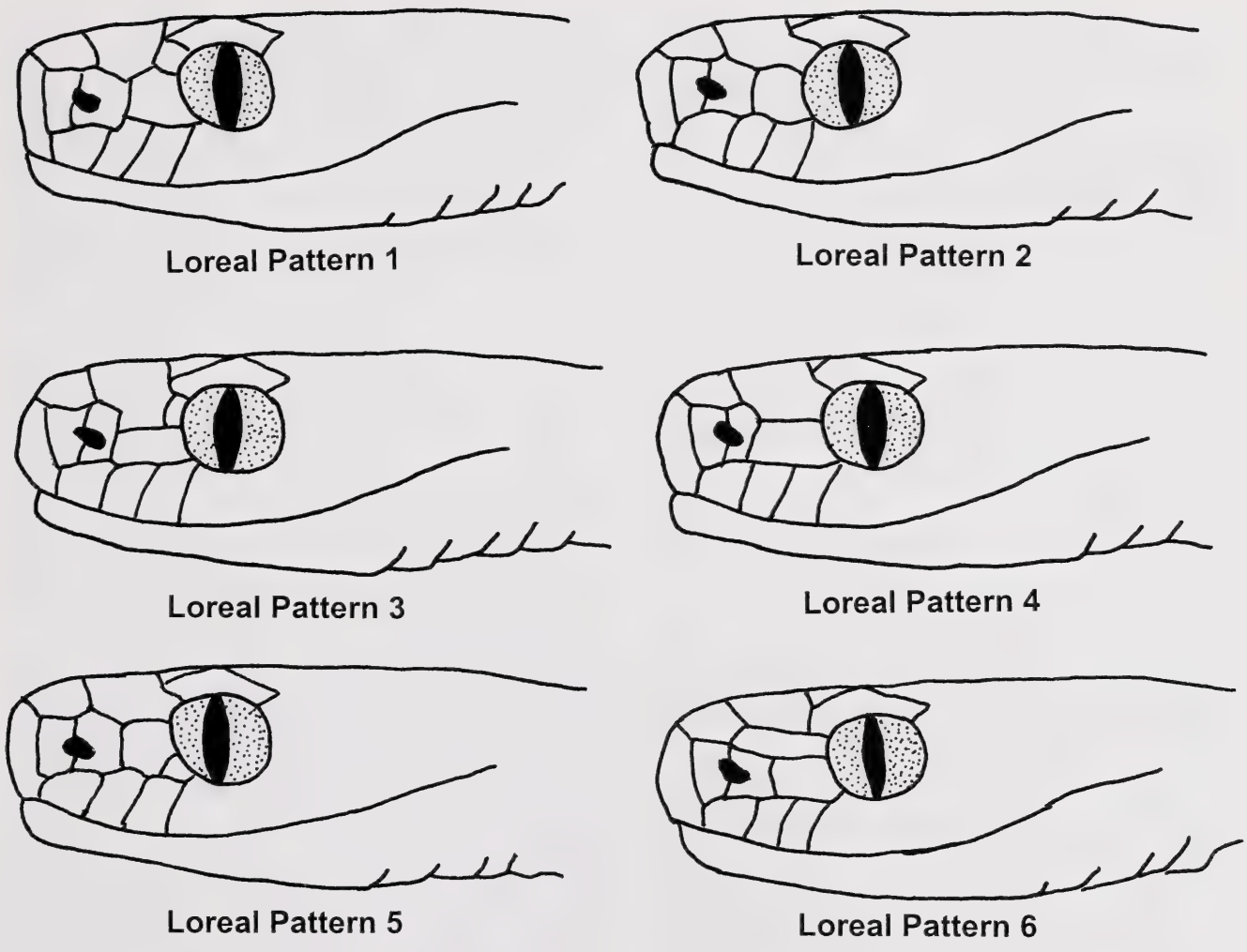

Figure 1. Variation in scale patterns in the loreal region of species of *Dipsas.* **Patterns 1 and 2:** loreal squarish or polygonal; separate preocular present above loreal (pattern 1) or fused with prefrontal scale (pattern 2). **Patterns 3 and 4:** loreal rectangular, much longer than tall; separate preocular present above loreal (pattern 3) or fused with prefrontal scale (pattern 4). **Patterns 5 and 6:** rare patterns; pattern 5 is similar to pattern 2 but has a small triangular preocular separated from the posteroventral corner of the loreal; pattern 6 has an elongate preocular above the loreal and extending from the eye to the internasal. Patterns 1 and 2 are the common patterns in *D. oreas,* with patterns 5 and 6 less frequent. Patterns 3 and 4 are characteristic of *D. elegans* and *D. ellipsifera.* See text for discussion.

between the sexes; see Tables 1–3). In these species, use of total segmental counts yields no insights that are not apparent from separate consideration of ventral and subcaudal numbers, specifically because the difference between the sexes with regard to total segmental counts is contributed entirely by the subcaudals; this fact is obscured when the subcaudal count is evaluated solely as a component of the total segmental count. On the other hand, in *D. elegans,* males have significantly greater numbers of ventrals and subcaudals than females, with virtually no overlap in the counts for either character between the sexes. As in *D. oreas* and *D. ellipsifera,* the use of total segmental counts in *D. elegans* reveals nothing that would not be seen by separate consideration of ventrals and subcaudals, each of which is strongly sexually dimorphic for this species. Moreover, it obscures the highly unusual pattern of sexual dimorphism in ventral counts in *D. elegans* (discussed later herein).

Thus, the use of total segmental counts elucidates no patterns of sexual dimorphism or interspecific differences within the *Dipsas oreas* group that would not be evident from separate analysis of ventral

and subcaudal numbers. It also potentially obscures other features, such as the relative contribution of ventrals or subcaudals to any revealed pattern, and atypical patterns of sexual dimorphism (as for *D. elegans*). Nonetheless, I report total segmental counts in the descriptions and summary data tables that follow so that others can evaluate their utility for themselves. Whether the approach of using total segmental counts yields generally useful insights into the systematics of *Dipsas* is not clear to me. A casual inspection of data for several other South American species (Table 4; unpublished data) indicated no particular utility over and above separate consideration of ventral and subcaudal counts for this small sampling of taxa.

THE *DIPSAS OREAS* COMPLEX: RESURRECTION OF *DIPSAS ELEGANS* AND *DIPSAS ELLIPSIFERA*

Cope (1868) described *Leptognathus oreas* from a specimen (holotype: ANSP 10115) obtained by James Orton with the type locality "elevated Valley of Quito" [Ecuador]. The "Valley of Quito" is the type locality for many amphibians and reptiles from Orton's large South American collections, but it has been misinterpreted by most authors dealing with his collections. It is clarified herein (see the account for *Dipsas oreas*).

Subsequent to Cope's description of *Dipsas oreas,* several taxa now perceived as related to it were described: *Leptognathus andrei* Sauvage (1884) with type locality "Loja, Nouvelle-Grenade"[2]; *D. elegans* (Boulenger, 1896) with type locality "Tehuantepec" [Mexico];, and *D. ellipsifera* (Boulenger, 1898) with type locality "Ibarra" [Ecuador]. These nominal taxa have remained poorly known since their descriptions. Peters (1960a) placed *D. elegans* and *D. ellipsifera* in his *oreas* group, but he had insufficient data to infer the relationships of *Leptognathus andrei.* Kofron (1982) provided photographs of the holotypes or syntypes of these forms and presented evidence that *Leptognathus andrei* Sauvage is a synonym of nominotypical *D. oreas,* a conclusion with which I concur on the basis of the photograph of the type and information provided by Kofron (see Table 3).[3]

The status of the nominal forms *Dipsas elegans* and *D. ellipsifera* and their relationship (if any) to *D. oreas* require further consideration. Contrary to reports in the literature, these three taxa are diagnosable from one another. Peters (1960a) recognized the similarity of the color patterns of *D. elegans* and *D. ellipsifera* but thought, erroneously, that *D. elegans* was a Mexican species because the original description (Boulenger, 1896: 452) stated that the holotype was from "Tehuantepec." Consequently, Peters assigned all Ecuadorian specimens with the distinctive *elegans–ellipsifera* pattern to *D. ellipsifera* (Peters, 1960a: 92). Peters' concept of *D. ellipsifera* therefore included specimens of *D. elegans,* even though he recognized the latter as a distinct species from Mexico. Subsequent discussions of these snakes (Kofron, 1982; Orcés and Almendáriz, 1987) have been misled by Peters' confusion of the two species in western Ecuador and by inadequate attention to sexual dimorphism and geographic origin of samples. This confusion, combined with tacit acceptance by most recent workers of specimen iden-

[2] After 1830, New Granada comprised Panama + Colombia, a result of the secession of Ecuador and Venezuela from Gran Colombia, which had existed for a short time subsequent to colonial independence from Spain in the early 19th century. Sauvage (1884) reported "Nouvelle-Grenade" as the type locality, but the data recorded in the MNHN catalogues for the holotype (MNHN 6285) explicitly include "Loja" according to R. Roux-Esteve as reported by Kofron (1982: 48–49).

[3] *Dipsas oreas* was, for many years, also confused with *Sibynomorphus mikanii* (e.g., *Sibynomorphus mikanii oreas* or *Dipsas mikanii oreas* reported from Ecuador by Amaral 1929a, "1929"b [1930] and Parker [1934, 1938]). This resulted from synonymy of the two species by Günther (1872) and Boulenger (1896: 453). The confusion was discussed by Peters (1960a: 93–94).

tifications in some older literature (e.g., Boulenger, 1896), has led to considerable uncertainty concerning differential characteristics of these nominal taxa and their respective distributions.

Peters' (1960a) confusion of two Ecuadorian species under the name *Dipsas ellipsifera* affected his assessment of variation within this species. For example, his ventral and subcaudal counts for males and females of "*Dipsas ellipsifera*" (Peters, 1960a: 87) are exceptionally broad for a species of snake having a small range in western Ecuador. Nonetheless, Peters (1960a: 91) recognized a distinctive geographic pattern to the variation within his concept of *D. ellipsifera*:

> The material available can be divided into two groups as to provenance, the first coming from the Río Mira drainage and referred to as the "typical population," and the other from the western slopes of the Andes in Ecuador, to the south of the Río Mira. . . . Although the indicated differences between these two populations suggest subspecific status, I am not assigning them a name, because no satisfactory holotype is available. . . . The most striking differences between the two populations are in counts involving body segments.

Peters goes on to detail differences between the Río Mira specimens and the others when samples are segregated by sex. However, he did not make the conceptual leap to recognizing distinct species on the basis of these populational differences. Nor did he recognize that the "other" population from the western slopes of the Andes represented *Dipsas elegans*, believing as he did that *D. elegans* was a Mexican species.

Kofron (1982) clarified much of the confusion engendered by the uncertain origin of the holotype of *Dipsas elegans*. He summarized evidence that the holotype of *D. elegans* came from western Ecuador on the basis of the known travels and contacts of Adolphe Boucard, who sold the specimen to the British Museum (Kofron, 1982: 47). Kofron also reviewed the erroneous association of the name of the collector, François Sumichrast, who collected in the vicinity of the Isthmus of Tehuantepec, with the type of *D. elegans*. The error was promulgated by Günther (1885–1902: 141) and continued in checklists and faunal works (e.g., Peters, 1960a: 86; Smith and Taylor, 1945) until Kofron discovered the mistake. The unfortunate association of Sumichrast's name with the specimen that ultimately became the holotype of *D. elegans* resulted in it being considered a Mexican species by Peters (1960a) and others (e.g., Smith and Taylor, 1945).

Kofron's (1982) conclusion that the holotype of *Dipsas elegans* most likely came from Ecuador was a major step toward resolving the systematics of these snakes. Nonetheless, because the type specimens of *D. ellipsifera* and *D. elegans* have nearly identical color patterns, Kofron (1982: 48) synonymized *D. ellipsifera* with *D. elegans*, which is the earlier name. He did not thoroughly consider other character variation in available samples of these snakes, particularly in the context of geographic origin and sex, even though some of these patterns had already been elucidated by Peters (1960a; see previous quotation).

Despite having examined much of the same material as Peters, Kofron (1982) used Peters' (1960a) data when comparing the scale counts of the holotype of *Dipsas elegans* with *D. ellipsifera*, apparently failing to realize that Peters had confused the two species under the name "*Dipsas ellipsifera*" and overlooking Peters' more detailed discussion of geographic variation within his concept of *D. ellipsifera*: "The ventral and subcaudal counts of [the holotype of] *D. elegans* (183, 95) are within the ranges of 155–187 ventrals and 72–105 subcaudals reported for *D. ellipsifera* by Peters (1960)" (Kofron, 1982: 47). Thus, Kofron (1982) accepted Peters' (1960a) characterization of "*Dipsas ellipsifera*," which included specimens of *D. elegans*; not surprisingly, characteristics of the holotype of *D. elegans* conformed well to this composite taxon. Kofron did not reexamine the meristic data of specimens segregated by sex and locality and failed to no-

tice a few other subtle differences between the two (see below). Peters (1960a), although he elucidated the pattern of geographic variation, did not differentiate the population samples as distinct taxonomic entities or associate the name "*Dipsas elegans*" with one of the population samples. Kofron (1982: 50) further suggested that "A comprehensive analysis of *D. oreas* and *D.* [*elegans*] may show the two to be subspecifically related, as I can distinguish the specimens . . . only by pattern." Kofron's (1982: 50) use of the name *D. ellipsifera* throughout the last paragraph of his text is an apparent lapsus for *D. elegans* in view of his synonymizing the former name with the latter earlier in the paper (Kofron, 1982: 48).

Orcés and Almendáriz (1987) acted on Peters' observations of geographic variation and examined additional specimens of both *Dipsas elegans* and *D. ellipsifera.* Unfortunately, in their reconsideration of the geographic pattern, they again lumped specimens by locality without regard to sex and thus failed to elucidate the correlation between sexual dimorphism in meristic data and geography that had been outlined by Peters (1960a). On the basis of average differences in meristic characters between population samples and little or no overlap in segmental counts between them, Orcés and Almendáriz (1987) maintained *D. elegans* and *D. ellipsifera* as distinct taxonomic entities but, following Kofron's (1982: 50) suggestion, considered them subspecies of *D. oreas* Cope. Orcés and Almendáriz provided the new combinations *Dipsas oreas elegans* and *Dipsas oreas ellipsifera.* The taxonomic justification was based on the broad overlap in ventral and subcaudal counts between nominotypical *D. oreas* and *D. elegans* (Orcés and Almendáriz, 1987: 138) and on the similar color patterns of *D. elegans* and *D. ellipsifera.*

The relationship, if any, of *Dipsas elegans* and *D. ellipsifera* to *D. oreas* warrants renewed scrutiny. Peters (1960a: 30–31) defined species groups on the basis of color pattern characteristics. This was unfortunate because color patterns are highly variable within some species of *Dipsas.* Nonetheless, Peters' *oreas* group included *D. elegans, D. ellipsifera,* and *D. oreas* by virtue of having a color pattern in which "the blotches are wider than the interspaces, with little contrast in color between them (pl. IVa) [and] the centers of the blotches are considerably lightened, which often gives the species an appearance of having paired ellipses on the sides. . . . The interspaces are rather heavily streaked and spotted with dark colors" (Peters, 1960a: 31).

A glance at the photograph that Peters chose to illustrate color patterns characteristic of the *oreas* group (Peters, 1960a: Plate IVa) shows that even this example does not fit the definition well (e.g., some of the interspaces are wider than the blotches and the the color pattern exhibits great contrast). Examination of only a few specimens will quickly erode confidence in Peters' definition of the *oreas* group. In all three species of the *oreas* group, the width of the blotches (or bands) varies along the length of the body; anteriorly, they are virtually always wider than the interspaces, but posteriorly, they are narrower than the interspaces. Most specimens of all three species have highly contrasting patterns (see later discussion of *D. oreas* for some exceptions, Cadle and Myers [2003: 21–25], the photograph of the holotype in Kofron [1982], and later discussion and illustrations herein).

The similarity and uniqueness of the color patterns of *Dipsas elegans* and *D. ellipsifera,* and their narrowly allopatric distributions (documented herein), suggest a close relationship between the two species. However, the similarity in segmental counts between *Dipsas elegans* and *D. oreas,* particularly among females (see Table 1), is of minimal consequence in assessing a possible relationship or conspecificity between them because many species of *Dipsas* have broadly overlapping scale counts (Cadle and Myers [2003] and subsequent discussions herein of *D. gracilis*). Thus,

there seems to be little to unify *D. elegans, D. ellipsifera,* and *D. oreas* as a "species group," Peters' (1960a) color pattern characteristic notwithstanding. The color patterns of *D. elegans* and *D. ellipsifera* in reality bear little resemblance to that of *D. oreas.* Moreover, *D. andiana,* which Peters (1960a, 1965) considered a synonym of *D. oreas,* seems to be more closely related to *D. nicholsi* of Panama than to *D. oreas* (Cadle and Myers, 2003: 32–34). As emphasized by Cadle and Myers (2003), interspecific relationships among species of *Dipsas* need to be reassessed with a broader, more comprehensive set of characters than currently exists. Thus, the species groups elaborated by Peters (1960a) can be considered categories only of convenience.

Nonetheless, as will be shown, all three species of the *oreas* group are unusual with respect to sexual dimorphism in ventral counts compared with typical colubrid patterns. *Dipsas oreas* and *D. ellipsifera* show no sexual dimorphism in ventral counts, whereas *D. elegans* is highly unusual in that males have higher ventral counts than females. Whether these characteristics are restricted to the *oreas* group or are more broadly distributed within *Dipsas* requires study of additional species. A casual survey of data for other species of *Dipsas* at hand (Table 4 for *D. gracilis* and several species considered by Cadle and Myers [2003]) suggests that unusual patterns of sexual dimorphism in segmental counts might prevail within this genus. Thus, with respect to Peters' "*oreas* group," I address questions concerning the proper definition and diagnoses of the included species without necessarily implying any phylogenetic unity to the group.

Despite their previous confusion in much of the previous literature, careful study shows that *Dipsas elegans, D. ellipsifera,* and *D. oreas* can be distinguished from one another by a combination of scutellational, color pattern, and dentition characteristics. For these reasons I resurrect *D. elegans* and *D. ellipsifera* from the synonymy of *D. oreas,* and recognize all three taxa as valid species. I herewith provide differential diagnoses for these species and summarize their systematics, geographical distributions, and natural history. A summary of variation in standard systematic characters for these species (Table 1) will be helpful in following the ensuing diagnoses and descriptions.

Dipsas ellipsifera (Boulenger) Figures 2–8

Leptognathus ellipsifera Boulenger, 1898: 117. Lectotype BMNH 1946.1.21.26 (Fig. 2, Table 2) designated herein. Type locality, "Ibarra" [Ecuador]. Werner, 1922: 197.

Sibynomorphus ellipsifer: Amaral, "1929"b [1930]: 197.

Dipsas ellipsifera: Peters, 1960a: 87. Peters, 1965: 3. Peters and Orejas-Miranda, 1970: 86.

Dipsas elegans, part: Peters, 1960a: 87, 91–92 (referred specimens from the western slopes of the Andes in Ecuador exclusive of those from the Río Mira drainage, specifically including those from "Camino a Mindo," "El Corazón," and "near Peñaherrera"). Kofron, 1982: 48. Miyata, 1982: 16.

Dipsas oreas ellipsifera: Orcés and Almendáriz, 1987: 138. Pérez-Santos and Moreno, 1991: 156.

Notes on the Type Series and Designation of a Lectotype

The syntypes of *Leptognathus ellipsifera* comprise four specimens obtained by W. F. H. Rosenberg and sent to the British Museum of Natural History: BMNH 1946.1.21.26–29 (original numbers 98.4.28.87–90). The original description (Boulenger, 1898) simply noted "several specimens." Data on the syntypes are presented in Table 2, and the largest male, BMNH 1946.1.21.26 (Fig. 2), is hereby designated the lectotype. The smallest of the paralectotypes, BMNH 1946.1.21.27, was illustrated by Kofron (1982: fig. 1), and the lectotype and female paralectotype (BMNH 1946.1.21.28) are illustrated herein (Figs. 2, 3). A fine artistic rendering of the head and anterior body of the female paralectotype (the largest specimen) was given in the original description (Boulenger, 1898: pl. XII, fig. 2).

The lectotype is an adult male in good

TABLE 1. COMPARISONS OF SIZE AND STANDARD CHARACTERS IN *DIPSAS ELLIPSIFERA*, *D. ELEGANS*, AND *D. OREAS*. FOR HEAD SCALES, EACH SIDE OF THE HEAD WAS SCORED SEPARATELY BECAUSE INDIVIDUAL SPECIMENS WERE FREQUENTLY BILATERALLY ASYMMETRICAL. TWO DATA SUMMARIES FOR *D. OREAS* DATA ARE PRESENTED (COLUMNS 3 AND 4): ECUADORIAN SPECIMENS ONLY (FOR DIRECT COMPARISON WITH *D. ELEGANS* AND *D. ELLIPSIFERA*; SEE TEXT) AND THE TOTAL SAMPLE (ECUADORIAN + PERUVIAN SPECIMENS OF *D. OREAS*; SEE TABLE 3 FOR ADDITIONAL BREAKDOWN OF DATA FOR *D. OREAS*). *N* = NUMBER OF SPECIMENS OR OBSERVATIONS; SVL = SNOUT TO VENT LENGTH.

			Dipsas oreas	
	Dipsas ellipsifera	*Dipsas elegans*	Ecuador	Total sample
Total length (SVL) (mm)				
Largest male	566 (417)	683+ (515+)	691 (509)	758 (547)
Largest female	630 (488)	782 (587)	827 (626)[1]	827 (626)
Tail length/total length				
Male	0.24–0.27	0.26–0.28	0.25–0.26	0.25–0.28
	0.25 ± 0.01 (*N* = 7)	0.27 ± 0.009 (*N* = 6)	0.26 ± 0.01 (*N* = 8)	0.26 ± 0.008 (*N* = 18)
Female	0.21–0.22	0.22–0.26	0.23–0.24	0.21–0.24
	0.215 ± 0.007 (*N* = 2)	0.24 ± 0.018 (*N* = 5)	0.24 ± 0.005 (*N* = 8)	0.24 ± 0.009 (*N* = 14)
Maxillary teeth	15 (*N* = 1)	17 (*N* = 6)	12 (*N* = 4)	12 (*N* = 6)
	16 (*N* = 2)	18 (*N* = 3)	13 (*N* = 7)	13 (*N* = 8)
	17 (*N* = 2)	19 (*N* = 2)	14 (*N* = 2)	14 (*N* = 9)
	18 (*N* = 1)	21 (*N* = 1)		
Dorsal scales	15-15-15 (*N* = 8)	15-15-15 (*N* = 9)	15-15-15 (*N* = 15)	15-15-15 (*N* = 35)
	16-15-15 (*N* = 1)	16-15-15 (*N* = 1)	16-15-15 (*N* = 1)	16-15-15 (*N* = 1)
		15-15-13 (*N* = 3)	15-15-13 (*N* = 1)	15-15-13 (*N* = 1)
		15-17-16 (*N* = 1)		15-17-15 (*N* = 1)
Ventrals				
Male	153–164	177–189	173–184	167–184
	157.4 ± 3.51 (*N* = 7)	181.5 ± 4.44 (*N* = 8)	178.6 ± 3.38 (*N* = 8)	175.7 ± 4.95 (*N* = 21)
Female	157–158	166–178	171–181	167–181
	157.5 ± 0.71 (*N* = 2)	172.4 ± 5.13 (*N* = 5)	178.2 ± 3.12 (*N* = 10)	175.8 ± 4.58 (*N* = 16)
Subcaudals				
Male	72–78	94–105	82–87	82–91
	74.8 ± 2.03 (*N* = 7)	98.0 ± 4.19 (*N* = 6)	85.3 ± 2.06 (*N* = 7)	86.6 ± 2.43 (*N* = 19)
Female	62–63	68–88	74–83	70–83
	62.5 ± 0.71 (*N* = 2)	80.0 ± 7.62 (*N* = 5)	76.4 ± 3.20 (*N* = 8)	76.1 ± 3.27 (*N* = 14)
Total segmental counts				
Male	229–242 (*N* = 7)	272–294 (*N* = 6)	258–271 (*N* = 7)	251–271 (*N* = 22)
Female	220 (*N* = 2)	237–260 (*N* = 5)	245–263 (*N* = 8)	241–263 (*N* = 14)
Anal scale	Single	Single	Single	Single

TABLE 1. CONTINUED.

	Dipsas ellipsifera	*Dipsas elegans*	*Dipsas oreas*	
			Ecuador	Total sample
Loreal pattern	3 (N = 16)	3 (N = 24)	1 (N = 12)	1 (N = 12)
	4 (N = 2)	4 (N = 2)	2 (N = 18)	2 (N = 44)
			5 (N = 4)	5 (N = 5)
				6 (N = 13)
Preoculars	0 (N = 2)	0 (N = 2)	0 (N = 18)	0 (N = 44)
	1 (N = 17)	1 (N = 24)	1 (N = 16)	1 (N = 30)
Postoculars	2 (N = 18)	1 (N = 2)	2 (N = 19)	1 (N = 4)
		2 (N = 23)	3 (N = 13)	2 (N = 39)
			4 (N = 2)	3 (N = 31)
				4 (N = 2)
Primary temporals	2 (N = 18)	1 (N = 4)	1 (N = 9)	1 (N = 13)
		2 (N = 20)	2 (N = 21)	2 (N = 42)
		3 (N = 1)	3 (N = 4)	3 (N = 18)
				4 (N = 1)
Secondary temporals	2 (N = 3)	2 (N = 4)	2 (N = 3)	2 (N = 4)
	3 (N = 15)	3 (N = 20)	3 (N = 24)	3 (N = 47)
		4 (N = 1)	4 (N = 6)	4 (N = 22)
Supralabials (touching eye)	6 (3–4) N = 1	6 (3–4) N = 2	7 (3–5) N = 7	6 (2–4) N = 1
	6 (4) N = 1	6 (4–5) N = 1	7 (4–5) N = 6	6 (3–4) N = 2
	7 (3–5) N = 1	7 (3–5) N = 1	8 (3–5) N = 4	7 (3–4) N = 1
	7 (4–5) N = 10	7 (4–5) N = 10	8 (4–5) N = 1	7 (3–5) N = 16
	8 (4–5) N = 3	8 (3–5) N = 1	8 (4–6) N = 13	7 (4–5) N = 18
	8 (4–6) N = 1	8 (4–5) N = 3	9 (4–6) N = 1	8 (3–4) N = 1
	8 (5–6) N = 1	8 (4–6) N = 4	9 (4–7) N = 1	8 (3–5) N = 6
		8 (5–6) N = 1		8 (4–5) N = 10
		9 (4–6) N = 1		8 (4–6) N = 16
		9 (4–7) N = 1		9 (4–6) N = 1
				9 (4–7) N = 1
Intralabials	8 (N = 1)	8 (N = 1)	9 (N = 1)	9 (N = 1)
	9 (N = 1)	9 (N = 3)	10 (N = 5)	10 (N = 7)
	10 (N = 12)	10 (N = 10)	11 (N = 15)	11 (N = 20)
	11 (N = 4)	11 (N = 6)	12 (N = 12)	12 (N = 31)
		12 (N = 5)	13 (N = 2)	13 (N = 16)
Number of dorsal bands/ blotches on body	30–39	26–46	19–30	17–30
	34.2 ± 3.56 (N = 9)	34.3 ± 5.81 (N = 13)	24.9 ± 2.96 (N = 17)	22.6 ± 3.38 (N = 34)

[a] The largest female of *D. oreas* is the holotype of *Leptognathus andrei* Sauvage, from measurements reported by Kofron (1982: 49) (not examined for this study).

Figure 2. *Dipsas ellipsifera* (Boulenger). Male lectotype in dorsal and ventral views (BMNH 1946.1.21.26; 349 mm SVL).

TABLE 2. STANDARD CHARACTERS OF THE LECTOTYPE AND PARALECTOTYPES OF *DIPSAS ELLIPSIFERA*. BILATERAL COUNTS ARE SEPARATED BY A SOLIDUS (LEFT/RIGHT). SVL = SNOUT TO VENT LENGTH.

	Lectotype BMNH 1946.1.21.26 male	Paralectotype BMNH 1946.1.21.27 male	Paralectotype BMNH 1946.1.21.28 female	Paralectotype BMNH 1946.1.21.29 male
Total length (SVL) (mm)	465 (349)	265 (202)	630 (488)	336 (254)
Tail length/total length	0.27	0.24	0.22	0.24
Maxillary teeth	18	—	16	—
Dorsal scales	16-15-15	15-15-15	15-15-15	15-15-15
Ventrals (and preventrals)	158 (2)	159 (3)	157 (1)	156 (2)
Subcaudals	73	75	63	74
Total segmental counts	231	234	220	230
Anal scale	Single	Single	Single	Single
Loreal pattern	3/3	3/3	3/3	4/3
Preoculars	1/1	1/1	1/1	0/1
Postoculars	2/2	2/2	2/2	2/2
Primary temporals	2/2	2/2	2/2	2/3
Secondary temporals	3/3	3/3	3/3	2/2
Tertiary temporals	4/4	3/4	3/4	3/3
Supralabials (touching eye)	7 (4–5)/7 (4–5)	8 (4–5)/7 (4–5)	7 (4–5)/8 (5–6)	7 (4–5)/6 (4)
Infralabials	10/10	11/11	10/10	11/10
Number of infralabials in contact behind mental	1 pair	2 pairs	1 pair	1 pair
Number of bands or blotches on body	39	38	31	30

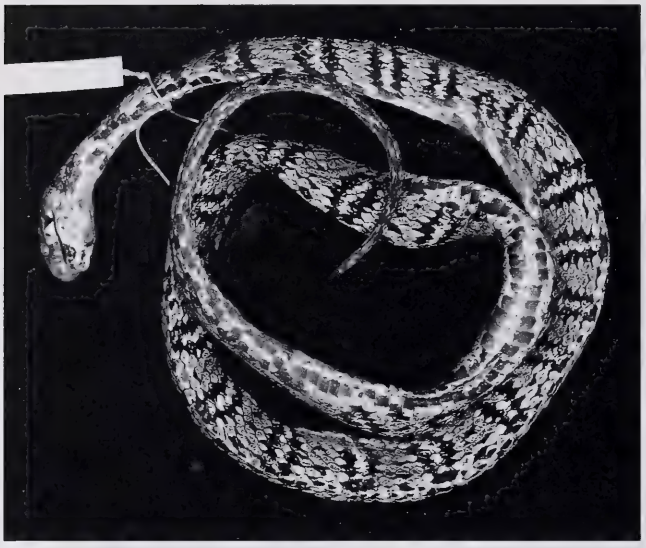

Figure 3. Female paralectotype of *Dipsas ellipsifera* (BMNH 1946.1.21.28; 488 mm SVL).

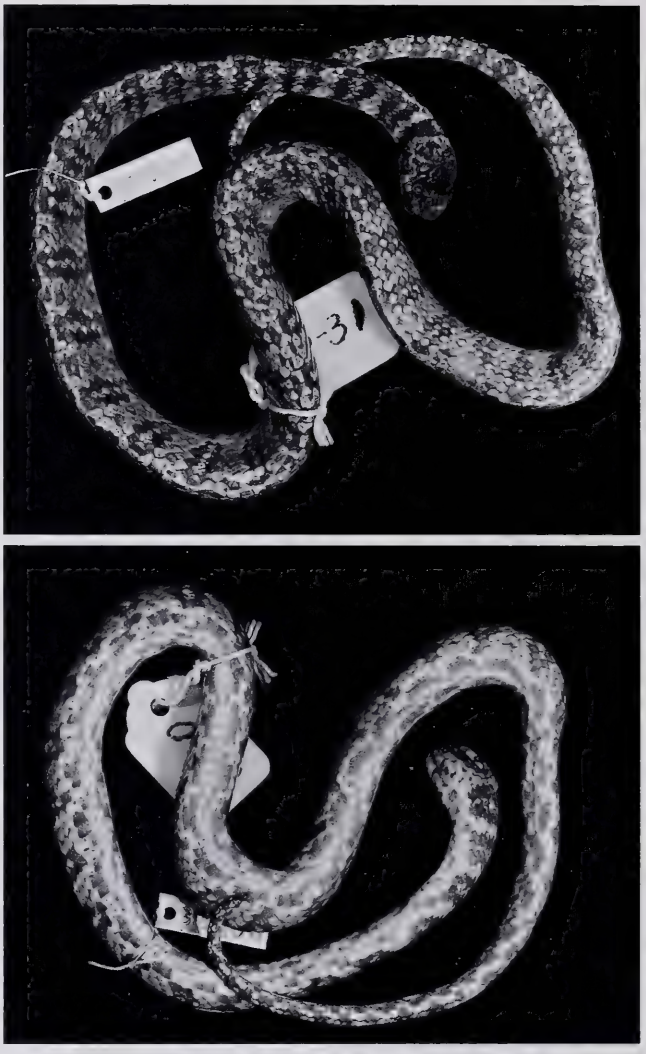

Figure 4. *Dipsas ellipsifera* (Boulenger). Dorsal and ventral views of UMMZ 83700, an adult from Pimampiro, Ecuador (349 mm SVL).

condition and has a color pattern and general characteristics typical of all specimens of *Dipsas ellipsifera* examined. In addition to details reported for the lectotype in Table 2, it is worth noting that the dorsal formula of 16-15-15 is a variation occasionally observed within *Dipsas*. The lectotype has a relatively longer tail (27% of total length) than other specimens of *D. ellipsifera* examined. Comments concerning the color patterns of the syntypes are given in the section on coloration below.

Diagnosis

Dipsas ellipsifera is characterized by a low number of ventrals (153–164 in seven males, 157–158 in two females) and subcaudals (72–78 in males, 62–63 in females). Its color pattern consists of 30 to 40 markings, each of which has a characteristic composition. Each marking typically appears as a closely spaced pair of black bars or bands with a central whitish area (Figs. 2–5, 7); edges of the markings are more or less vertical. The markings may be continuous across the vertebral region, forming complete bands, or contralateral markings may fail to meet in the vertebral region, forming a series of lateral bars. The anterior five or six markings are broader than more posterior ones and are equivalent to, or broader than, the light interspaces. Posterior markings are narrower than the interspaces.

Dipsas ellipsifera differs from all other species of *Dipsas* in western Ecuador by its low number of ventrals and subcaudals and additionally differs from all species except *D. elegans* in color pattern (see Table 1 and the key accompanying this report). *Dipsas andiana, D. gracilis,* and *D. temporalis* all have >180 ventrals, >80 subcaudals, and patterns that do not involve narrow bands or bars with light centers. *Dipsas oreas* has >165 ventrals, >65 subcaudals, and a different color pattern (see below). Additional commentary is warranted concerning the most similar spe-

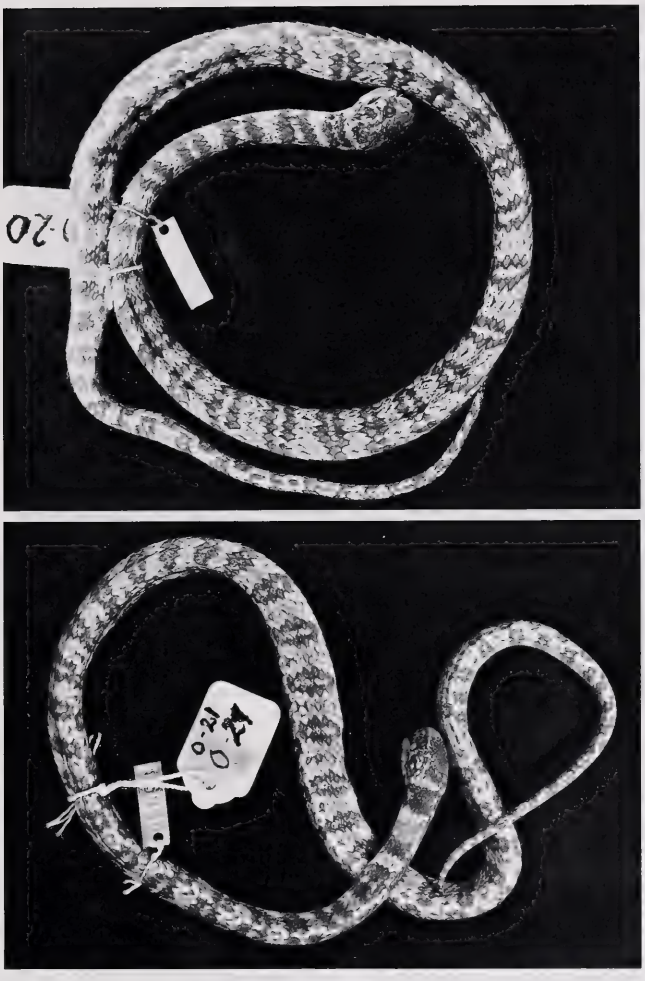

Figure 5. *Dipsas ellipsifera* (Boulenger). Dorsal views of representative adult specimens from Pimampiro, Ecuador. **Top:** UMMZ 83697 (386 mm SVL). **Bottom:** UMMZ 83698 (357 mm SVL).

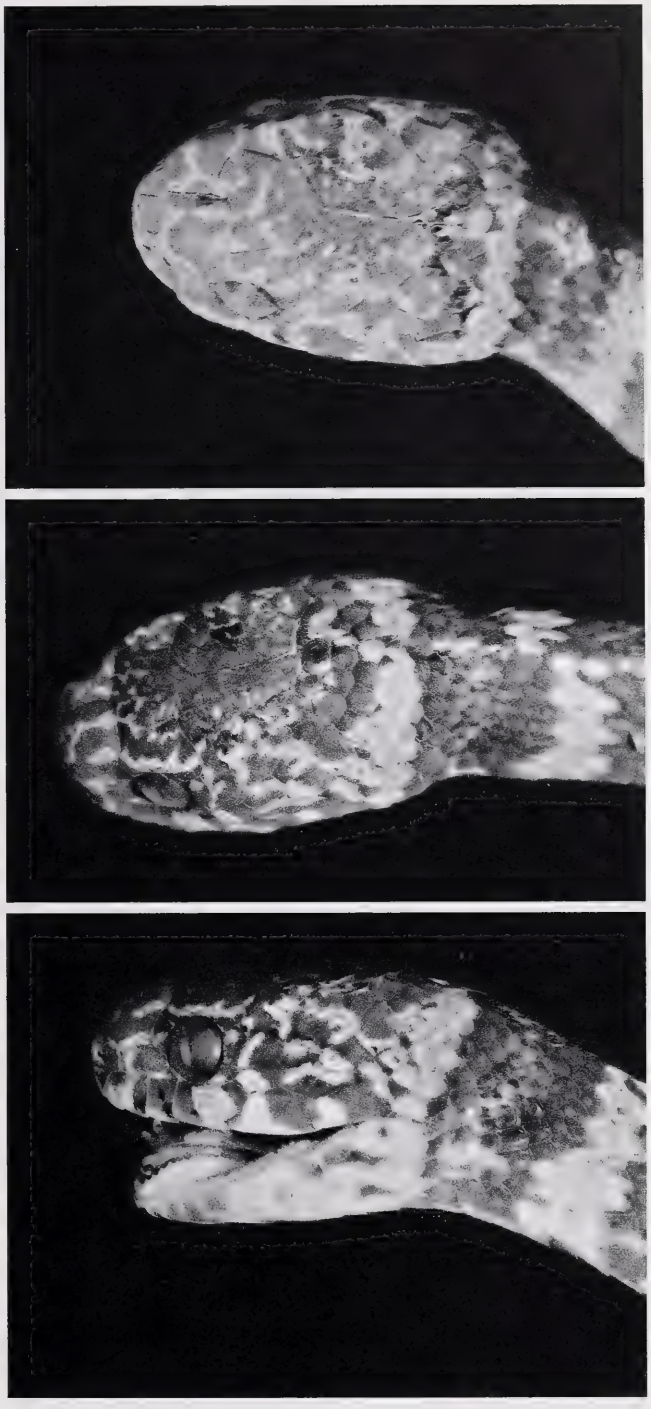

Figure 6. Head patterns of *Dipsas ellipsifera* (Boulenger). **Top:** UMMZ 83697. **Middle and bottom:** UMMZ 83698 (dorsal and lateral). Both specimens from Pimampiro, Ecuador.

cies, *D. elegans*, in view of their similar color patterns and the previous confusion of the two species (e.g., Kofron, 1982; Peters, 1960a). The distinctions are most clearly seen by separately comparing the sexes.

Dipsas ellipsifera differs from *D. elegans* (see Table 1) in having fewer ventrals (*D. elegans*: 177–189 in males; 166–178 in females) and subcaudals (*D. elegans*: 94–105 in males; 68–88 in females), a smaller relative eye size, and a differently shaped head (Figs. 6, 10). The head of adult *D. ellipsifera* is small relative to body size and has rounded canthal and temporal regions, whereas the head of adult *D. elegans* is larger, blocky, and has angular canthal and temporal regions. On the basis of a few observations for *D. ellipsifera*, it seems that small juveniles of this species (≤210 mm snout–vent length [SVL]) already manifest the adult color pattern (e.g., Fig. 7), whereas small juveniles of *D. elegans* (Figs. 11, 12) have solid dorsal bands that only develop light centers somewhat later

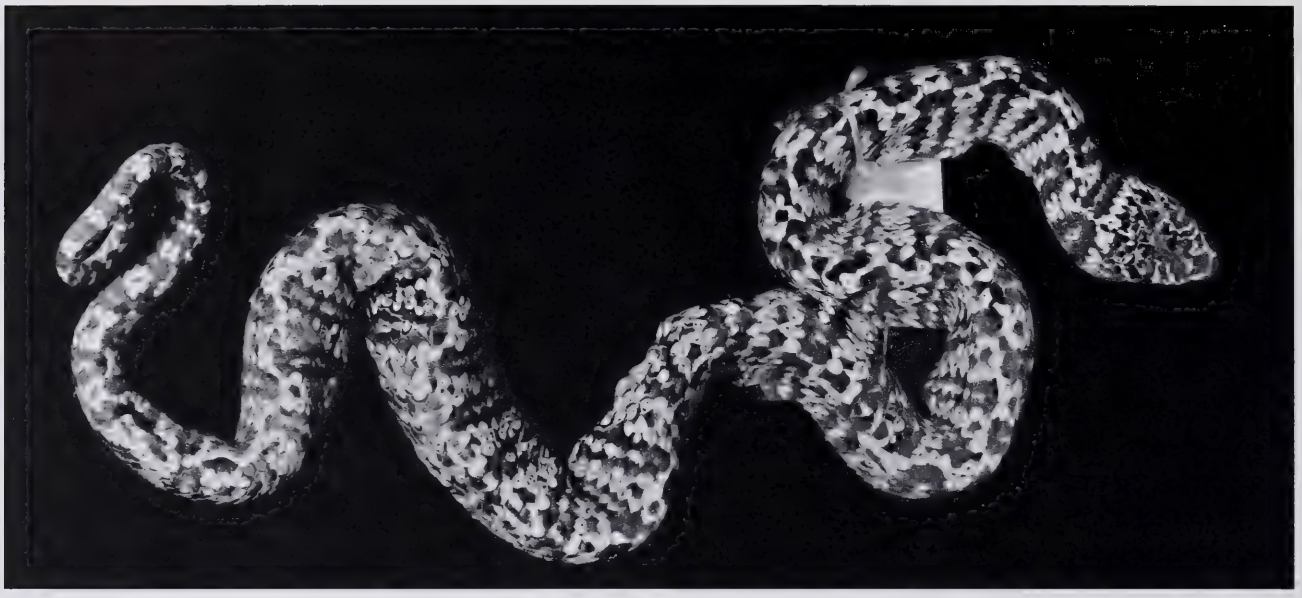

Figure 7. *Dipsas ellipsifera* (Boulenger). A small juvenile from the type locality, Ibarra, Ecuador (MCZ 8431, 210 mm SVL).

(see color descriptions in the species accounts).

Description

Characteristics of *Dipsas ellipsifera* are summarized in Table 1.

Size, Scutellation and Description. The largest specimen is a female 630 mm total length, 488 mm SVL. Largest male 566 mm total length, 417 mm SVL. Tail 24–27% of total length in seven males, 21–22% in two females. Body strongly compressed. Dorsal scales in 15-15-15 rows (rarely 16-15-15). Vertebral scale row approximately 2–2¼× the width of paravertebral rows. Ventrals 153–164 (averaging 157) in seven males; 157–158 (averaging 157.5) in two females. Males and females apparently not sexually dimorphic in ventral number. One to three preventrals precede the ventral series (see Myers, 2003, for discussion). Subcaudals 72–78 (averaging 75) in seven males, 62–63 (averaging 62.5) in two females. Total segmental counts 229–242 in seven males, 220 in two females. An elongate rectangular loreal and a small preocular border the anterior edge of the eye in most specimens; preocular superior to loreal (Fig. 1: loreal pattern 3). Preocular sometimes fused with prefrontal, which then borders the eye above the loreal (Fig. 1: loreal pattern 4). Head scales highly variable (Table 1): postoculars 2, primary temporals 2, secondary temporals usually 3 (sometimes 2). Supralabials 6–8 with varying combinations bordering the eye (Table 1); the most common pattern is 7 supralabials with 4–5 bordering the eye. Infralabials usually 10 (range 8–11). Either one pair ($N = 5$) or two pairs ($N = 3$) of infralabials in contact behind the mental. Two pairs of squarish chin shields followed by one or two pairs of offset gular scales that are wider than long. Maxillary teeth 15–18 ($N = 6$).

Color in Life. Unknown.

Color and Pattern in Preservative. In addition to illustrations herein, other illustrations of *Dipsas ellipsifera* include a detail of the midbody pattern of an adult male (Peters, 1960a: pl. IVa; UMMZ 83699, 417 mm SVL); dorsal and ventral views of a juvenile male paralectotype, BMNH 1946.1.21.27 (Kofron, 1982: fig. 1; 138 mm SVL); and an artistic rendering of BMNH 1946.1.21.28 in the original description (Boulenger, 1898: pl. XII, fig. 2).

The dorsal ground color of adults is dull pale brown or grayish with 30–39 paired dark brown bands or bars on the body (Figs. 2–5, 7). Each band or bar consists of a pair of bold, blackish, more or less

vertical markings separated by a narrow whitish strip. In some specimens the contralateral markings meet in the vertebral region, forming more or less complete bands, although the vertebral region tends to be invested with dark pigment so that the pale central regions of the markings are interrupted. In others (e.g., MCZ 8431; Fig. 7), contralateral markings fail to meet middorsally, forming lateral bars with pale centers that are closed off on their dorsal edges by black pigment. The markings have vertical edges and extend ventrally to the first scale row or the outer edge of the ventrals. Contralateral markings are frequently offset virtually the entire length of the body (e.g., Fig. 7) or on the posterior body only (most specimens). The markings (i.e., each black–white–black triplet) are 5–6 scale rows in width anteriorly but narrow to about 3 rows by midbody. Interspaces anteriorly are narrower than the bands or bars (approximately 3 scale rows), whereas they are wider than the markings posteriorly (5–6 scale rows). The venter is dull grayish brown with a dense covering of dark brown squarish markings that tend to be concentrated toward the outer edges of the ventrals, sometimes forming longitudinal arrays (Figs. 2–4).

The top and sides of the head are heavily marked with irregular dark markings on a pale brown ground color (Fig. 6). The markings are so extensive in some specimens that most of the top of the head is a solid dark brown, with just occasional light areas of the ground color showing through as fine reticulations or vermiform marks. Upper and lower labials are pale brown with dark brown spotting, but the dark stippling often is not especially concentrated along suture lines as in many species of snakes.

Two small juveniles (MCZ 8431, 210 mm SVL; BMNH 1946.1.21.27, 138 mm SVL) have patterns identical to those of adults, but more contrasting (Fig. 7; Kofron, 1982: fig. 1). The ground color is grayish white, and the dark markings are dark chocolate brown to blackish. The dorsal markings have pale centers and appear as blackish vertical bars (or narrow ellipses) enclosing whitish centers. Interspaces between the markings are whitish, but individual scales are speckled with tiny irregular dark brown flecks. The top of the head of MCZ 8431 is whitish with heavy reticulations and irregular spots so that much of the top and sides of the head are dark. The gular regions and venter are whitish with a pattern of bold irregular spots and blotches; on the venter these tend to form bold longitudinal streaks. If these two specimens are representative of very small individuals of *Dipsas ellipsifera,* this species appears already to have the adult color pattern even as small juveniles, a contrast with the developmental pattern in *D. elegans* and *D. oreas* (see the following species accounts for discussion). In the last two species, smallest juveniles have solid bands that develop pale centers during early juvenile ontogeny, thus acquiring the adult patterns sometime after hatching.

Hemipenis

The following description is based on the inverted organ of UMMZ 83697 examined in situ. The organ had previously been slit along its medial edge and the retractor muscle had been cut distal to its point of division.

Total length of the organ is 18 mm and it is slightly bilobed distally. The retractor muscle is divided proximally for 4 mm. The sulcus spermaticus (in the lateral wall of the organ) divides 9 mm from the base of the organ within the capitulum; the tips of its branches end approximately 1 mm short of the distal tips of the lobes. The basal region of the organ is sparsely ornamented with minute spines. The midsection has a battery of enlarged hooked spines encircling the organ just proximal to the capitulum; the battery is about 3 spines across around the entire organ. The capitulum is set off by a distinct overhang and is completely ornamented distally with

well-developed papillate calyces. However, the proximal papillae, especially those adjacent to the fork of the sulcus spermaticus and those fringing the overhang, have mineralized tips. A very large (8 mm long) nude pocket extends from the base of the organ to the battery of spines; its distal end is nestled within the proximal spines of the battery. The pocket is on the dorsal surface of the inverted organ (=the lateral surface of the everted organ relative to the sulcus spermaticus). The pocket has a large lobe on its absulcate edge and a smaller lobe on its sulcate edge; these lobes also bear minute scattered spines. The asulcate side of the organ (medial side of the inverted organ) bears 3 enlarged spines in a transverse row, which are separated by a gap (ornamented with minute spines) from the battery of spines on the midsection.

The hemipenis of *Dipsas ellipsifera* is similar in many details to hemipenes of other snakes of the tribe Dipsadini that have been described (review in Cadle and Myers, 2003: 14–15). Features common to hemipenes of the Dipsadini include well-developed papillate calyces on the capitulum, an encircling battery of enlarged spines on the midsection, a relatively unornamented base, and a very large nude pocket proximally on either the asulcate or lateral surface of the organ. The nude pocket in *D. ellipsifera* is exceptionally long, 44% of the length of the organ. In other species examined by Cadle and Myers (2003: 15) the pocket was approximately 33% of the length of the organ. However, observations in Cadle and Myers (2003) were based on everted organs and it is not possible to know the relative proportions of the nude pocket in the everted hemipenis of *D. ellipsifera* because hemipenial tissue expands differentially upon eversion (see Myers and Cadle, 2003). The proximally divided retractor muscle in *D. ellipsifera* suggests that its everted hemipenis may be somewhat more bilobed than everted hemipenes of either *D. elegans* or *D. oreas* described later herein. The degree of bilobation apparently varies among species of *Dipsas* (Cadle and Myers, 2003: 14–15).

Distribution and Natural History

Dipsas ellipsifera is known only from the valley of the Río Mira in extreme northwestern Ecuador (Fig. 8). All reported specimens are from Imbabura Province; the Río Mira divides Imbabura from Carchi Province, and the species may also occur in the latter province. Elevations for the two localities for which specimens were examined in this study are 2,000 and 2,211 m, but Orcés and Almendáriz (1987) reported an elevational range of 572–2,600 m for this species (see *Specimens Examined and Locality Records*). Several specimens collected by Philip Hershkovitz (UMMZ 83697–700) were obtained in June and August, but most specimens are not accompanied by specific collection dates.

The type locality of *Dipsas ellipsifera*, Ibarra, lies at 2,211 m elevation in a dry rain shadow valley of the western Andes. Rosenberg (quoted in Hartert, 1898) described the vicinity of Ibarra at the time the syntypes were collected as ". . . open, and for the most part cultivated," seemingly quite different from a nearby locality at a lower elevation to the west, Paramba (=Hacienda Paramba; Paynter, 1993), which Rosenberg described as "densely forested." Orcés and Almendáriz (1987: 138) stated the following concerning localities for *D. ellipsifera*: ". . . [the localities] are found in the subtropical and temperate zones. The region in question is for the most part semiarid with shrubby vegetation; in a few cases epiphytic and parasitic plants are present. The temperature varies from 18° to 22° C and the precipitation from 500 to 1,000 mm." Lita, the most western locality and the lowest elevation (572 m) from which *D. ellipsifera* has been recorded (Orcés and Almendáriz, 1987), lies in the region of very humid lowland rain forest characteristic of northwestern Ecuador.

Because Peters (1960a) confused some

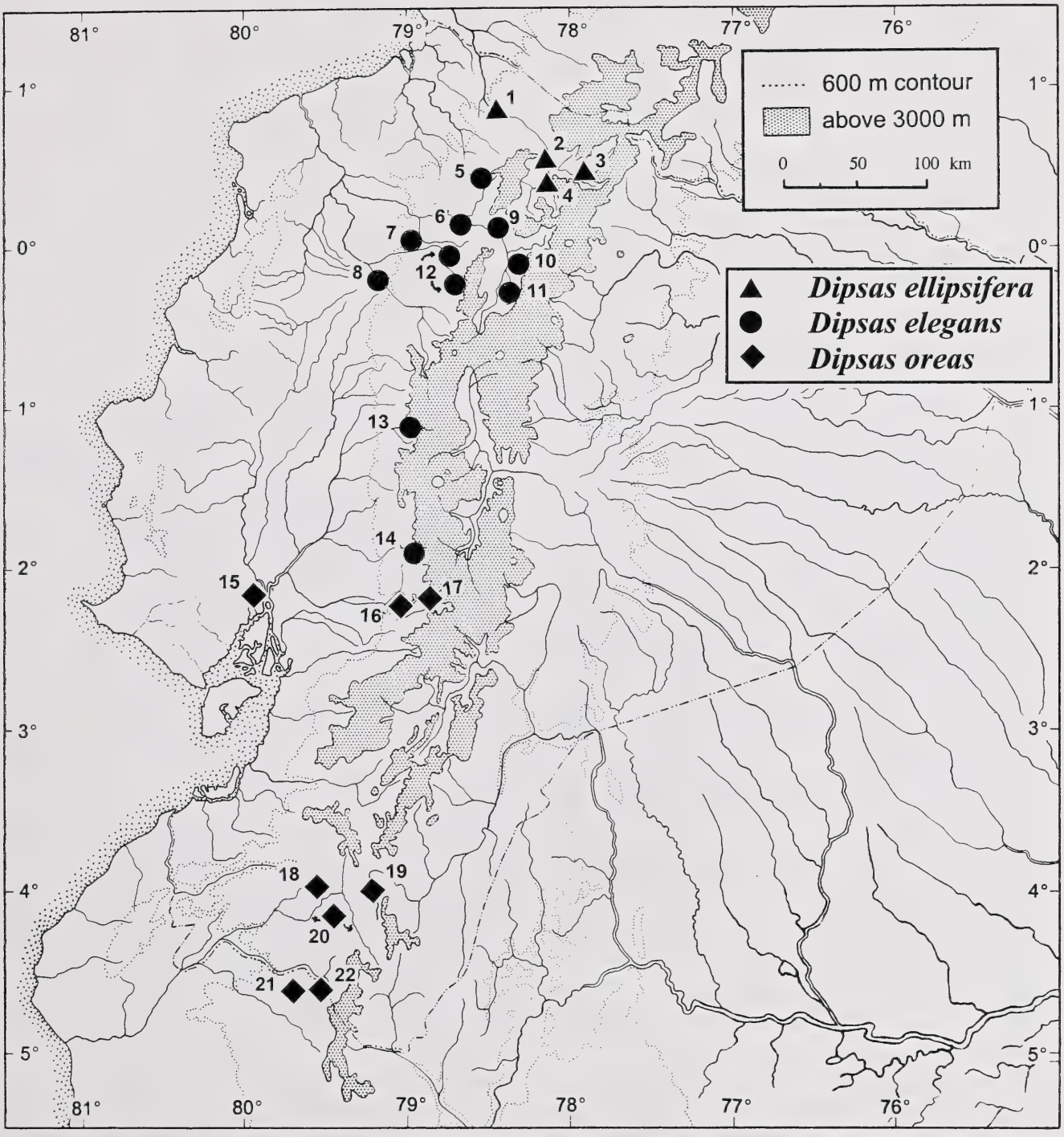

Figure 8. Locality records for *Dipsas ellipsifera*, *D. elegans,* and *D. oreas* in western Ecuador and extreme northern Peru. See Figure 23 for other known Peruvian localities for *D. oreas*. A few symbols for *D. elegans* and *D. oreas* represent pairs of contiguous localities; otherwise, all localities considered reliable are plotted (see text and list of specimens and localities). Numbered localities. *Dipsas ellipsifera*: **(1)** Lita (Orcés and Almendáriz, 1987); **(2)** Chachimbiro (Orcés and Almendáriz, 1987); **(3)** Pimampiro; **(4)** Ibarra (type locality). *Dipsas elegans*: **(5)** Peñaherrera; **(6)** Nanegal Grande and Pacto; **(7)** Río Saloya; **(8)** Santo Domingo de los Colorados; **(9)** Perucho (Orcés and Almendáriz, 1987); **(10)** El Quinché (Orcés and Almendáriz, 1987); **(11)** Cumbayá and Tumbaco (Orcés and Almendáriz, 1987); **(12)** Mindo (north) and Chiriboga (south; Orcés and Almendáriz, 1987); **(13)** Corazón; **(14)** Pallatanga. *Dipsas oreas*: **(15)** Guayaquil; **(16)** Huigra/Río Chiguancay and Río Chanchan valley; **(17)** Alausí (Despax, 1911); **(18)** Velacruz; **(19)** Loja; **(20)** Río Catamayo; **(21)** Ayabaca (Peru); **(22)** Cerro Aypate (Peru).

specimens of *Dipsas elegans* with *D. ellipsifera* (see above nomenclatural history), several specimens and associated localities he listed for *D. ellipsifera* are known or probable errors. UMMZ 98073 (Peñaherrera-Intag) is here referred to *D. elegans.* Three specimens that Peters (1960a) cited from the Escuela Politécnica Nacional (EPN, Quito), EPN 719 ("camino a Mindo") and EPN 717–718 ("El Corazón"), are probably equivalent to specimens referred herein to *D. elegans,* which Peters obtained from Orcés and later catalogued at the USNM (see *Specimens Examined and Locality Records* and footnote 9).

Dipsas elegans (Boulenger) Figures 8–13

Leptognathus mikanii, part: Günther, 1885–1902: 141. Boulenger, 1896: 454: variant C ("*L. oreas,* Cope"), specimens *c, d* from "W. Ecuador" (=BMNH 60.6.16.73) and "Pallatanga, Ecuador" (=BMNH 80.12.5.267; Fig. 13), respectively [misidentifications].

Leptognathus elegans Boulenger, 1896: 452. Holotype BMNH 1946.1.21.77 (original number 71.2.7.36). Type locality unknown, "Tehuantepec" [Mexico], in error. The type locality was discussed by Kofron (1982), who concluded that the specimen must have come from Ecuador (see above discussion). Orcés and Almendáriz (1987: 139) unjustifiably inferred that Perucho (Pichincha Province) "could be considered the type locality." The holotype was illustrated by Kofron (1982: Fig. 1).

Sibynomorphus elegans: Amaral, 1926: 9. Amaral, 1929a: 29. Amaral, "1929"b [1930]: 197.

Leptognathus maxillaris Werner: Amaral, 1929a: 29, "1929"b [1930]: 197.[4] Kofron (1982: 46) examined the holotype of *L. maxillaris* and stated that it was "badly faded and cannot be allocated to any known form at this time . . . [but] possibly the same taxon as *L. elegans.*"

Dipsas elegans: Parker, 1926: 206. Smith and Taylor, 1945: 51. Peters, 1960a: 86. Peters, 1965: 3. Miyata, 1982: 16.

Dipsas oreas, part: Peters (1960a: 94) based on BMNH 1940.2.20.32 from "Río Saloya, Ecuador" [misidentification]. Identification of the same specimen (as "*Dipsas oreas oreas*") also accepted by Orcés and Almendáriz (1987: 140).

Dipsas ellipsifera: Kofron, 1982:46.

Dipsas oreas elegans: Orcés and Almendáriz, 1987: 138. Pérez-Santos and Moreno, 1991: 154.

Notes on the Holotype

Photographs of the holotype of *Leptognathus elegans* (BMNH 1946.1.21.77) were presented by Kofron (1982: fig. 1) and accurate artistic renderings were given in the original description (Boulenger, 1896: pl. XVIII, fig. 3). The specimen has a color pattern typical of other specimens of *Dipsas elegans* with SVL greater than about 200 mm (see discussion below on ontogeny of color pattern and Figs. 11 and 12 for examples). Its presumed provenance from western Ecuador was discussed previously herein.

The holotype is a subadult male with the following characteristics (differences from those reported by Kofron, 1982: 46–47 reported in parentheses): Total length, 301 mm. Tail length, 78 mm. SVL, 223 mm. Tail as a proportion of total length, 26%. Dorsal scales in 15-15-15 rows. Ver-

[4] Laurent (1949) and Smith and Taylor (1945) did not wholeheartedly accept Amaral's synonymy. However, they questioned the synonymy primarily because the holotype of *Leptognathus maxillaris* differs from *Dipsas elegans* by characters that are now known to be highly variable within species of *Dipsas* (e.g., labial counts, patterns of scales in the temporal region, and number of infralabials in contact behind the mental). Peters (1960a: 49) pointed out these issues but thought the problem needed additional study (he maintained *maxillaris* distinct from *elegans*).

The holotype of *Leptognathus maxillaris* was said to be from "Tabasco, Mexico," and Amaral (1929a,"1929"b [1930]) considered it a synonym of *D. elegans,* in part, because the type locality of *L. elegans* was understood (erroneously) to be "Tehuantepec" [Mexico]. Werner (1909: 279–280) reported the following characteristics (among others) for the holotype of *L. maxillaris*: 180 ventrals, 84 subcaudals, 6 supralabials (3 + 4 touching the eye), 40 "coffee brown" bands on the body, total length 335 mm, tail length 70 mm. Laurent (1949) stated that the holotype was a female. These characteristics and others reported by Laurent (1949) and Werner (1909) are consistent with characteristics of female *D. elegans,* although the relative tail length (21% of total length) is slightly lower than in specimens I examined (Table 1). As with other poorly illustrated type descriptions of *Dipsas* spp., reexamination of the holotype of *D. maxillaris* will ultimately be necessary to confirm its identity, although this could be problematic if, as reported by Kofron (1982), no elements of pattern remain on the specimen.

tebral row about 2× the width of paravertebral rows. Ventrals, 182 + 1 preventral (183). Subcaudals, 95. Anal scale single. Preoculars, 1/1, situated superior to an elongate loreal, which touches the eye. Postoculars, 2/2. Temporals, 2 + 3 + 3/2 + 2 + 3. Loreal pattern 3 (small preocular superior to an elongate loreal). Supralabials, 8/8 with 4–5 touching the eye on each side. Infralabials, 10/10; one pair of infralabials meeting behind the mental scale. Two pairs of subequal squarish chin shields followed by two pairs of offset gular scales. Maxillary teeth 17 (18) (my count taken on the left side; not stated by Kofron).

Dorsal bands or blotches on body 40, each band consisting of a pair of bold, blackish, vertical bars with crenulated edges, between which is a narrow white bar (thus giving the appearance of dark bands with pale central portions). Anterior bands are 3–4 dorsal rows wide, narrowing to 3 rows by midbody and 2 rows posteriorly. Central white portion of bands 1 scale or less in width. The first five bands are not offset but all remaining bands are slightly to greatly offset, failing to join middorsally; the offset increases posteriorly. The dorsal bands extend down to outer edges of ventrals. The venter has bold squarish blotches that tend to align longitudinally into irregular streaks spanning several ventral scales. The top of the head is dark brown, concentrated more centrally (more white pigment on prefrontals, internasals, supraoculars, and peripheral parietal region). Many white fine reticulations and irregular marks are on the top of the head.

In addition to these characters, Kofron (1982) reported additional details, such as head measurements, head scale proportions, color pattern details (herein incorporated into the general description), and dentary teeth (22).

Diagnosis

Dipsas elegans is characterized by a moderate number of ventrals (177–189 in eight males, 166–178 in five females) and subcaudals (94–105 in males, 68–88 in females). Its color pattern consists of 26 to 46 narrow dark dorsal bands which, except in small juveniles (see below), have light centers (Figs. 9, 11–13). The bands have more or less vertical edges. The anterior five or six bands are broader than more posterior bands and are equivalent to, or broader than, the light interspaces. Posterior bands are narrower than the interspaces.

Dipsas elegans differs from other species in western Ecuador except *D. ellipsifera* by its distinctive color pattern (each band consisting of a pair of dark edges enclosing a contrasting pale center). *Dipsas gracilis* and *D. temporalis* have very broad black bands without pale centers. *Dipsas andiana* has a distinctive U- or V-shaped marking on the top of the head and a pattern of lateral blotches that lack pale centers (Cadle and Myers, 2003). The two species most often confused with *D. elegans* are *D. ellipsifera* and *D. oreas*. *Dipsas ellipsifera* differs from *D. elegans* in having fewer ventrals and subcaudals and a different head shape (see above diagnosis for *D. ellipsifera*).

Orcés and Almendáriz (1987), following a suggestion by Kofron (1982: 50), considered *Dipsas elegans* only subspecifically distinct from *D. oreas*. However, Kofron's suggestion was based only on the similarity in segmental counts in the two species, which is common among species of *Dipsas*. Several characteristics distinguish these species when data are analyzed separately for males and females to account for sexual dimorphism.

Dipsas elegans and *D. oreas* have quite distinct color patterns and I am unaware of intermediate specimens (compare Figs. 9, 13 with Figs. 14–19 for general dorsal patterns; Fig. 10 with Figs. 20–22 for head patterns). A specimen from the southernmost known locality for *D. elegans* (Fig. 13) has a color pattern typical of all specimens from farther north (e.g., Fig. 9), and it is equally distinct from the northernmost specimens of *D. oreas* from an adjacent

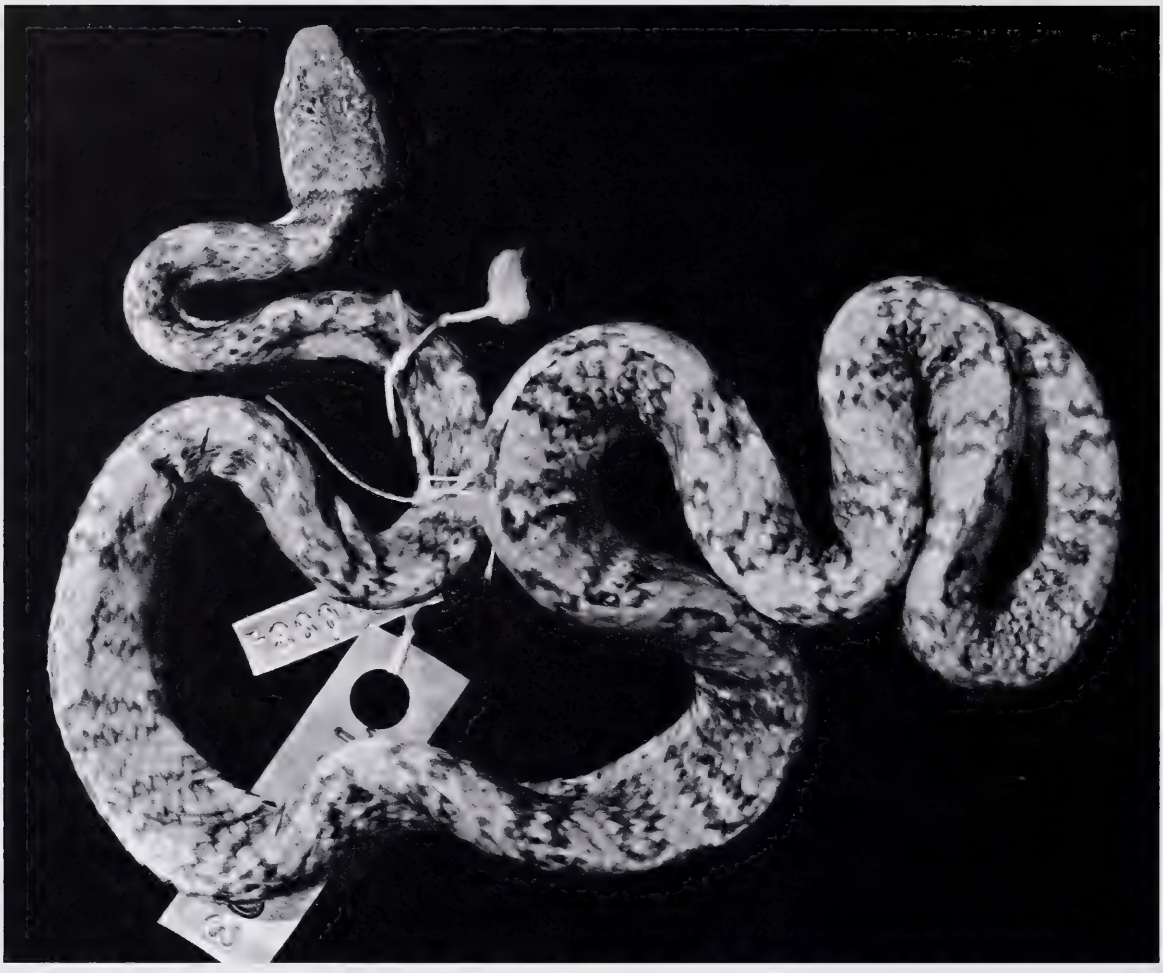

Figure 9. *Dipsas elegans* (Boulenger). Dorsal view of an adult male from Pichincha Province, Ecuador (USNM 210934, 501 mm SVL).

valley (see Fig. 8, localities 14, 16–17). The scutellation and body proportions of *D. elegans* and *D. oreas* are similar, whether the reference sample of *D. oreas* includes only Ecuadorian specimens (the most pertinent comparison to *D. elegans*) or the entire sample of *D. oreas* from Ecuador and Peru (Table 1). Average subcaudal number in male *D. oreas* is significantly less than in male *D. elegans* and their ranges do not overlap. Other segmental counts are similar between the two species, although average values differ (Table 1).

An additional characteristic distinguishing *Dipsas elegans* and *D. oreas* is an unusual pattern of sexual dimorphism in *D. elegans*. *Dipsas elegans* is strongly sexually dimorphic in both ventral and subcaudal counts, whereas *D. oreas* is sexually dimorphic only in subcaudal counts (Table 1). Additionally, the pattern of sexual dimorphism in ventral counts in *D. elegans* is observed infrequently among colubrids: male *D. elegans* have significantly greater numbers of ventral scutes than females (Table 1), the reverse of the common pattern in snakes (Shine, 1993).[5] In contrast,

[5] Species in which male ventral counts are greater than in females are uncommon, but this is a derived character for some putative clades, such as the Neotropical xenodontine tribe Tachymenini (*Tachymenis, Thamnodynastes, Tomodon, Pseudotomodon, Ptychophis, Gomesophis,* and *Calamodontophis*; Bailey, 1967, 1981). The relationships of the Tachymenini are unclear, but no specific relationship to the Dipsadini or Dipsadinae is indicated, despite similarities among some of the included species, such as male superiority in ventral number and a propensity to consume gastropods in Dipsadini and some Tachymenini, for example, *Tomodon* (Bailey, 1981; Gallardo, 1972, and references therein). Some other genera

the pattern of sexual dimorphism in subcaudal counts in *D. elegans* is typical of the general pattern in colubrids; males have significantly greater subcaudal counts than females, and the ranges of subcaudal counts for males and females are entirely nonoverlapping.

A few other subtle characteristics also distinguish *Dipsas elegans* from *D. oreas* (characteristics given first for *D. elegans* followed by those for *D. oreas*; Table 1): Maxillary tooth number (17–21 vs. 12–14), number of bands/blotches on the body (26–46 vs. 17–30), supralabials touching the eye (usually 2 vs. usually 3, but these patterns are highly variable), and loreal pattern (pattern 3 predominant, or pattern 4 vs. patterns 1 and 2 predominant, or patterns 5 or 6). Despite these other differences, color pattern is the most obvious accessible difference between *D. elegans* and *D. oreas,* and it is distinctive except for small juveniles (approximately <200 mm SVL) of both species, which are similarly patterned with solid bands (Figs. 11, 12, 17). In such cases, careful attention to sex, scutellational variation, head color pattern (see below), and maxillary tooth number is usually decisive in differentiating these species. See additional comments on comparisons of juvenile color patterns of these two species below (*Color and Pattern of Juveniles in Preservative*).

Description

Variation in standard systematic characters for *Dipsas elegans* is summarized in Table 1.

Size, Scutellation and Dentition. The largest specimen is a female 782 mm total length, 587 mm SVL. Largest male 683+ mm total length (tail incomplete), 515 mm SVL. Tail 26–28% of total length in males, 22–26% of total length in females. Body strongly compressed. Dorsal scales usually in 15-15-15 rows, but 3 of 14 specimens examined showed a posterior reduction to 13 rows, and one specimen each had the unusual patterns of 15-17-16 or 16-15-15 rows (see Peters, 1960a: 90, for additional discussion). Vertebral scale row 1.5–2× the width of paravertebral rows, relatively wider in juveniles than adults. Ventrals 177–189 (averaging 181) in eight males, 166–178 (averaging 172) in five females. This pattern of sexual dimorphism is the reverse of the common pattern in colubrids (see footnote 5). One or two preventrals precede the ventral series (see Myers, 2003, for discussion). Subcaudals 94–105 (averaging 98) in six males, 68–88 (averaging 80) in five females. Total segmental counts 272–294 in six males, 237–260 in five females. Usually an elongate loreal and a small preocular bordering the anterior edge of the eye (Fig. 1: loreal pattern 3); preocular superior to loreal. Preocular sometimes fused with the prefrontal, resulting in loreal pattern 4 (Fig. 1). Head scales variable: postoculars usually 2 (occasionally 1); primary temporals usually 2 (range 1–3); secondary temporals usually 3

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of Tachymenini consume lizards or frogs (Bailey, 1981; personal observations). Among other putative synapomorphies, genera of Tachymenini are viviparous (stated as oviparous by Bailey [1967] but corrected by Bailey [1981]).

On the basis solely of hemipenial morphology, Zaher (1999) left the position of the Tachymenini as "Dipsadinae incertae sedis," and other workers have concluded that they "appear to be dipsadines" (e.g., Harvey and Muñoz, 2004). However, this association is contradicted by biochemical data (Cadle, 1984a; Vidal et al., 2000), which clearly ally three of the genera (*Thamnodynastes, Pseudotomodon, Tomodon*) to the South American xenodontine clade of Cadle (1984a) (=Xenodontinae of Zaher [1999] in large part). Although these genera lack the two hemipenial synapomorphies of "Xenodontinae" *sensu* Zaher, they similarly lack synapomorphies of Dipsadinae except, in some species, a relatively distal division of the sulcus spermaticus. However, this character varies within some colubrid genera, including Tachymenini (e.g., *Thamnodynastes* and *Tachymenis* among the Tachymenini), *Taeniophallus* (Xenodontinae according to Cadle [1984a], Myers and Cadle [1994], and Vidal et al. [2000]; incertae sedis according to Zaher [1999]), and *Geodipsas* (Pseudoxyrhopinae *sensu* Zaher, 1999). Hemipenial morphology evolves just as other anatomical characters, and it is highly unlikely that all species of large, diverse clades such as Dipsadinae or Xenodontinae will retain all characters synapomorphic for the clades (=characters plesiomorphic within the clade).

(range 2–4); supralabials 6–9, usually with supralabials 4 and 5 bordering the eye, but this characteristic is highly variable (Table 1); infralabials 8–12. Either one pair (N = 8) or two pairs (N = 5) of infralabials in contact behind the mental. Two or three pairs of squarish chin shields, followed by one or two pairs of gular scales, which are often subequal and offset. Maxillary teeth 17–21 (N = 12).

Most specimens of *Dipsas elegans* are from localities near the equator (Fig. 8), but specimens from the extreme ends of the distribution are, in some respects, unusual in some scutellation characteristics that may reflect geographic patterns (sample sizes are too small to analyze trends). BMNH 80.1.5.267 (Fig. 13), a female from the southernmost locality, Pallatanga (Fig. 8: locality 14), has the lowest subcaudal count (68) of all specimens (78–88 in other females), and a ventral count at the lower end of the range (169, compared with 166–178 in other females). I considered the possibility that this specimen might be *D. oreas,* in part because its locality is closest to the distribution of *D. oreas* (Fig. 8). However, its color pattern is typical of other *D. elegans* (details in the following section) and unlike the color pattern of *D. oreas.* Moreover, its ventral and subcaudal counts would be low for *D. oreas* as well. Other characteristics of this specimen are also more typical of *D. elegans* (see Table 1): maxillary teeth 17, two supralabials touching eye, and loreal pattern 4. A female (USNM 210939) from the next northern locality (Corazón, Fig. 8: locality 13) has the lowest ventral count of all females (166), but a subcaudal count (84) that is more typical for female *D. elegans.*

The northernmost locality for *Dipsas elegans,* represented by a male (UMMZ 92073), has both the highest ventral (189) and subcaudal (105) counts I recorded for this species. However, Orcés and Almendáriz (1987) reported the upper range of subcaudals for this species as 107 (sex and locality not given). These data for specimens at the northern and southern extent of the range of *D. elegans* suggest that higher ventral and subcaudal counts may pertain to the northern part of the range of the species, with lower counts in the southern part.

Color in Life. Unknown.

Color and Pattern of Adults in Preservative. In *Dipsas elegans,* the dorsal ground color is pale brown with a series of 26–46 dark brown bands and/or bars on the body, each marking having a pale center (Figs. 9, 13). The markings have more or less vertical edges and extend ventrally to the first scale row or the outer edge of the ventrals. Anterior markings are about 5 scales rows in width, narrowing to about 3 rows by midbody, and are usually complete across the vertebral region (there is frequent incursion of dark pigment middorsally so that the central pale areas are interrupted). Posterior bands are frequently offset middorsally, forming a series of lateral bars (Fig. 13). Interspaces anteriorly are narrower than the bands (approximately 3 scale rows) but are wider than the bands posteriorly (5–6 scale rows). The venter is dull grayish brown with a dense covering of dark brown squarish markings that tend to be concentrated toward the outer edges of the ventrals, sometimes forming longitudinal arrays. The dorsal pattern of *D. elegans* is essentially identical to that of *D. ellipsifera,* but the centers of the bands in *D. elegans* usually are a pale brown to tan (in preservative), rather than whitish, as in *D. ellipsifera.*

The top and sides of the head are marked heavily with irregular dark markings on a pale brown ground color (Fig. 10). The markings are so extensive in some specimens that most of the top of the head is a solid dark brown with occasional light areas of the ground color showing through. Juveniles tend to have more solidly dark-colored heads than adults. Upper and lower labials are pale brown with dark brown irregular spotting, often not concentrated along suture lines. Often the dark pigment on the supralabials is concentrated below

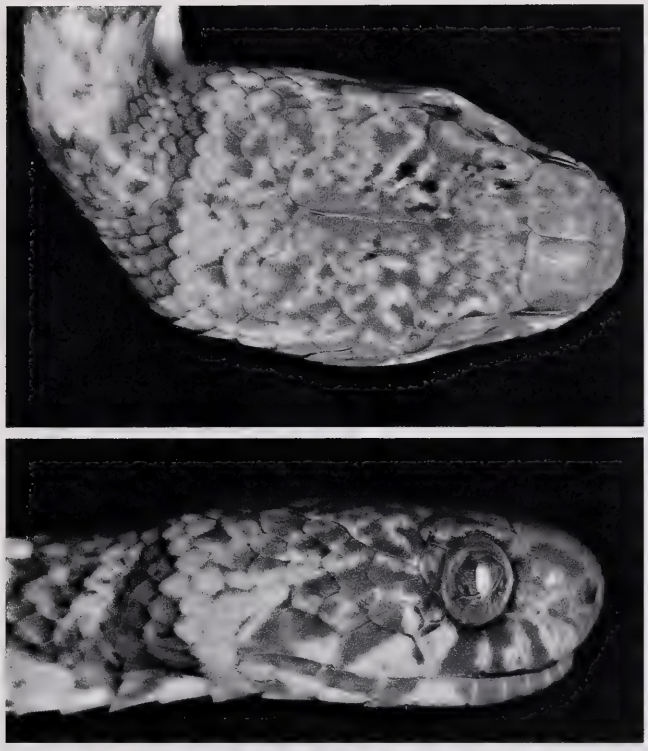

Figure 10. Head pattern in *Dipsas elegans* (Boulenger). Dorsal and lateral views of the head of USNM 210934.

the eye and on the posterior supralabials. In a few specimens, the dark pigment on the posterior supralabials extends diagonally toward the eye so as to form an irregular and indistinct postocular bar, but no individuals have a distinct postocular bar.

The following specimen is exemplary of the typical adult color pattern of *Dipsas elegans*.

BMNH 80.12.5.267 (see Fig. 13; Pallatanga, Chimborazo Province, Ecuador. Female, 452 mm SVL). Anterior bands 3.5 to 4 dorsal scale rows wide at their widest points; 2 rows wide at midbody and posteriorly. The first three dorsal bands and the sixth are complete middorsally; all others are incomplete and offset. The vertebral scale row is about 1.3× as wide as paravertebral rows. Dorsal blotches are dark-edged with pale centers, and more or less vertical (but jagged) edges. Interspaces are pale grayish brown, each scale heavily flecked with fine dark brown specks.

The top of the head is pale yellowish brown, marked with bold irregular spots all over; lacking the finer speckling that is present in most other specimens of *D. elegans*. The posterior edge of the head cap is marked with a narrow (1.5 scales wide) irregular edge in which dark pigment is more concentrated; following this is a pale nape collar about two scales wide, then the first neck band. Supra- and infralabials are pale with bold blackish marks, somewhat concentrated along suture lines.

The venter is heavily checkered with bold squarish blotches, with a slight tendency for these to align into irregular longitudinal streaks (but not as great a tendency as in some other specimens of *D. elegans*).

Color and Pattern of Juveniles in Preservative. The dorsal markings of *Dipsas elegans* apparently develop pale centers during early juvenile ontogeny, a phenomenon that also occurs in *D. oreas* (see subsequent species account). The dorsal bands of the juvenile holotype of *D. elegans* (223 mm SVL) already have light centers and a pattern similar to adults (see Kofron, 1982: fig. 1). Four smaller juveniles have bands in which there is no perceptible lightening: USNM 210938 (184 mm SVL), USNM 210961 (192 mm SVL), USNM 285957 (179 mm SVL), and BMNH 1940.2.20.32 (187 mm SVL) (Figs. 11, 12). Some lightening of the bands is apparent in two slightly larger individuals: in UMMZ 92073 (201 mm SVL; Fig. 12) lightening of the bands is barely apparent and is evident primarily on the anterior, wider bands; in USNM 210939 (199 mm SVL; Fig. 11), all of the bands have light centers. The last pattern is typical of adult *D. elegans* (Figs. 9, 13). Thus, small juveniles of *D. elegans* (<200 mm SVL) have solid bands, whereas the development of pale centers to the dorsal bands, and concomitant acquisition of adult color pattern, begins at approximately 200 mm SVL.

The following is a typical example of the color pattern of a small, solidly banded juvenile *Dipsas elegans* in preservative.

BMNH 1940.2.20.32 (Río Saloya, Pichincha Province, Ecuador. Female, 187 mm SVL). The dorsal pattern consists of regular, *solid* dark bands on pale ground color (no lightening of any dorsal bands). Bands are widest at midflank and narrow toward the ventrals and (less so) toward the vertebral scale row. Anterior bands are about 4 dorsal scale rows wide at their broadest point (the first band is 5 rows), narrowing to about 3 rows by midbody and continuing thus to the vent. Ventrally, the bands narrow to 3 scale rows wide on the anterior body, and to 2 rows wide on the posterior body; they encroach onto the outer edges of the ventrals.

The top of the head down to upper edges of supralabials is solid dark gray with a few scattered very indistinct irregular paler areas. Supralabials are about 50% covered with dark markings, which is not especially concentrated along sutures lines. Infralabials are mostly dark. An indistinct pale collar about 2 scales wide is between the dark head cap and the first neck blotch.

Ventral scutes are pale, with a pair of squarish blotches on the outer edges of most; the aligned blotches form irregular (and interrupted) series of broad lines on each side of the venter.

Small juveniles of *Dipsas elegans* with solid dorsal bands might be confused with juveniles of *D. oreas*, which also have solid bands. However, *D. elegans* typically has many more bands than *D. oreas* (compare Figs. 11, 12, 17), and the head patterns of the two species also provide differential characteristics. The top of the head in juvenile specimens of *D. elegans* is patterned with dark gray (?blackish in life) mottling

→

Figure 11. Juvenile patterns in *Dipsas elegans* (Boulenger). **Top to bottom:** USNM 210961, 192 mm SVL (Pichincha Province, Ecuador); USNM 210939, 199 mm SVL (Cotopaxi Province, Ecuador); USNM 210938, 184 mm SVL (Cotopaxi Province, Ecuador). The two smaller specimens (top and bottom) show no perceptible lightening of the central parts of the bands, whereas the lightening is very apparent in the middle specimen.

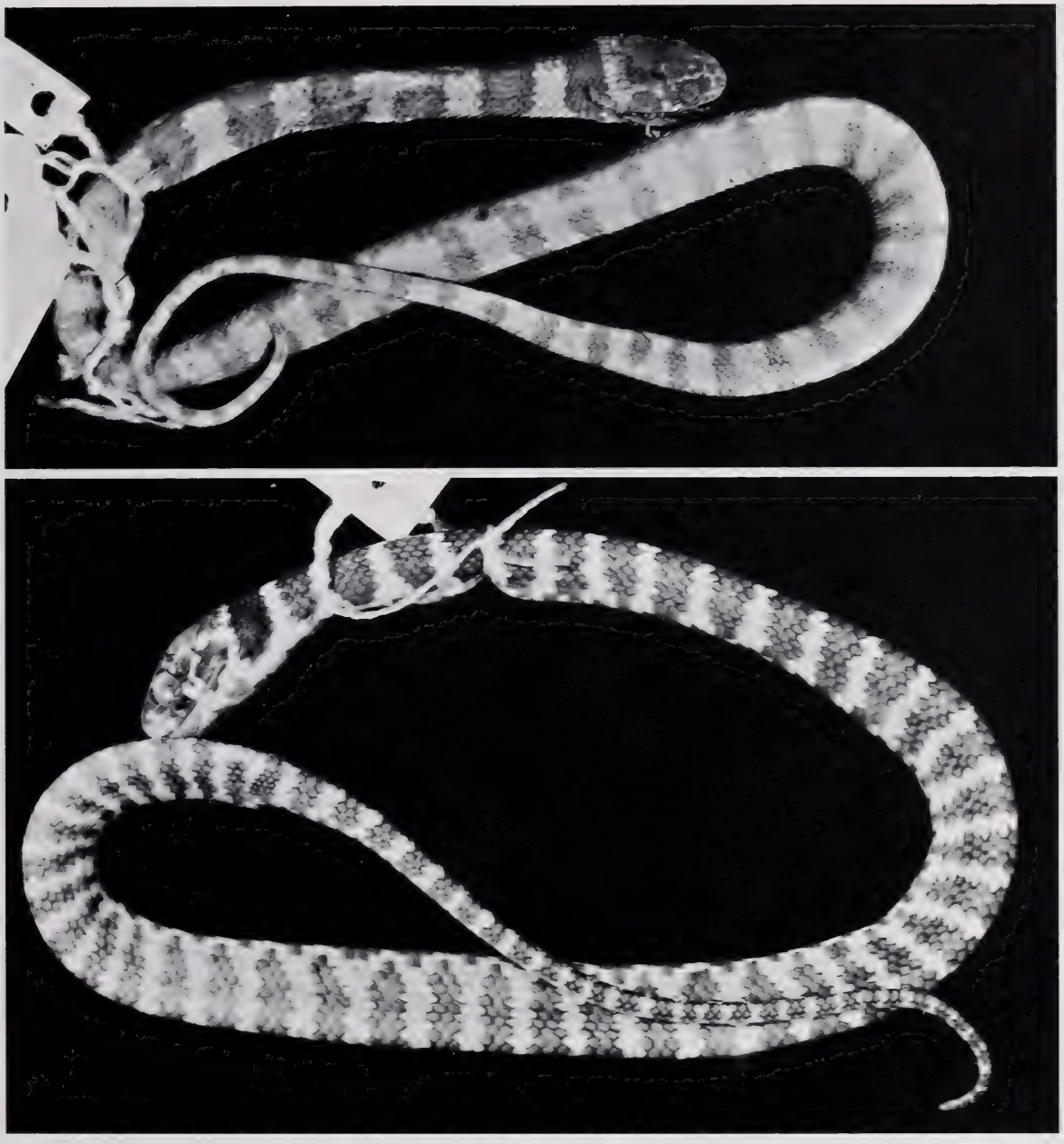

Figure 12. Juvenile patterns in *Dipsas elegans* (Boulenger). **Top:** UMMZ 92073, 201 mm SVL (Imbabura Province, Ecuador) showing some lightening apparent in bands on the anterior body. **Bottom:** USNM 285957, 179 mm SVL (Pichincha Province, Ecuador), in which no lightening of the central parts of the bands is apparent.

or reticulations on a pale brown or grayish ground color (the mottling may be so extensive as to color most of the top of the head with dark brown, especially in the parietal region). Juvenile *D. oreas* typically have paired dark elongate blotches in the parietal region, which is also characteristic of most adults (Figs. 16, 20; see also Cadle and Myers, 2003: 24, figs. 9, 10, 12). Moreover, juveniles of the two species differ by the other characteristics given in the diagnosis, including in loreal pattern (typically pattern 3 in *D. elegans*; typically pattern 1 or 2 in Ecuadorian *D. oreas*) and maxillary tooth number (Table 1). For example, maxillary tooth counts for seven juveniles of *D. elegans* (179–201 mm SVL) were 17–21; tooth counts for eight juveniles of *D. oreas* (150–193 mm SVL) were 12–14.

Hemipenis

The hemipenes of the holotype of *Dipsas elegans* (BMNH 1946.1.21.77) had

been previously exposed by ventral incision, and the right organ had been slit on its ventral surface. The following description is based on this specimen. It should be emphasized that, because the holotype is a juvenile, spines were not mineralized, and some other details perhaps differ from the adult condition (e.g., calyces appeared poorly developed, which might be either a product of the state of preservation or its juvenile condition, and spines in general had rather blunter tips than would be expected in a mature hemipenis).

The organ is very slightly bilobed at the tip (<1 mm), fully capitate, and extends to the level of the middle of subcaudal 8. The major retractor muscle is not divided at its insertion. The capitulum is ornamented with calyces bearing papillae; a distinct fringe of papillae borders the overhang separating the capitulum from the midsection. The capitulum appears to extend far less proximally on the asulcate than on the sulcate side and is more poorly delimited on the former. The sulcus spermaticus divides just inside the border of the capitulum. The midsection of the hemipenis has a battery of blunt spines (about 3–4 spines across, broader adjacent to the sulcus spermaticus than on the asulcate side). The blunt appearance of the spines is conceivably due to the juvenile state of the specimen; the more proximal spines in the battery have more pointed tips than more distal ones, possibly reflecting some mineralization of more proximal spines. Mineralization of the spines in colubrid hemipenes proceeds from proximal to distal on the organ (Cadle, 1996: 43–44; Myers and Cadle, 2003). Thus, it would not be surprising to observe more heavily mineralized spines on the proximal portion of a juvenile hemipenis.

The battery of spines is separated from the capitulum by a narrow gap of nude tissue (broader on the asulcate side). A poorly delineated but large basal nude pocket is present proximally; it is bordered distally by a pair of large spines, each of which is larger than any in the midsection battery, and a weakly developed lobe on one side. The proximal portion of the organ appears nude, but the presence of minute spines cannot be ruled out.

Distribution and Natural History

Dipsas elegans is distributed in the lowlands and on the slopes of the Andes in western Ecuador from just north of the Equator in Imbabura Province (0°21′N) to approximately 2°S latitude (Fig. 8). Most localities are in the foothills or western slopes of the Cordillera Occidental, although Orcés and Almendáriz (1987) reported localities well over 2,000 m in upper reaches of the Río Guayllabamba east of the city of Quito (El Quinche, Cumbayá, and Tumbaco; Fig. 8: localities 10, 11). Recorded elevations for collecting localities are 500–1,820 m for specimens examined during this study, but localities reported by Orcés and Almendáriz (1987: 139) are higher: 1,500–2,643 m.

Two of four specimens that Boulenger (1896: 454) referred to "*Leptognathus mikanii*" variant C, which he considered equivalent to "*L. oreas*, Cope," are *Dipsas elegans*: specimens *c* and *d* from "W[estern] Ecuador" and "Pallatanga, Ecuador," respectively BMNH 60.6.16.73 and 80.12.5.267 (the other two, specimens *a* and *b* are, indeed, *D. oreas*). The Pallatanga specimen (Fig. 13) represents the southernmost record of *D. elegans* (Fig. 8: locality 14), and it has low ventral and subcaudal counts compared with other specimens (see *Description*).

A small juvenile (USNM 285957; 179 mm SVL) was collected 20 February 1979 "about 1900 hr near a small stream with waterfall along roadside; about 2 m up on the face of a road cut—moving on outer edge of vegetation about 15 cm from soil" (Roy W. McDiarmid, field notes). The specimens examined were collected in February, April, May, July, and October.

Orcés and Almendáriz (1987: 139) summarized the ecological circumstances for localities of *Dipsas elegans* as follows (see similar quotation in the account for *D. el-*

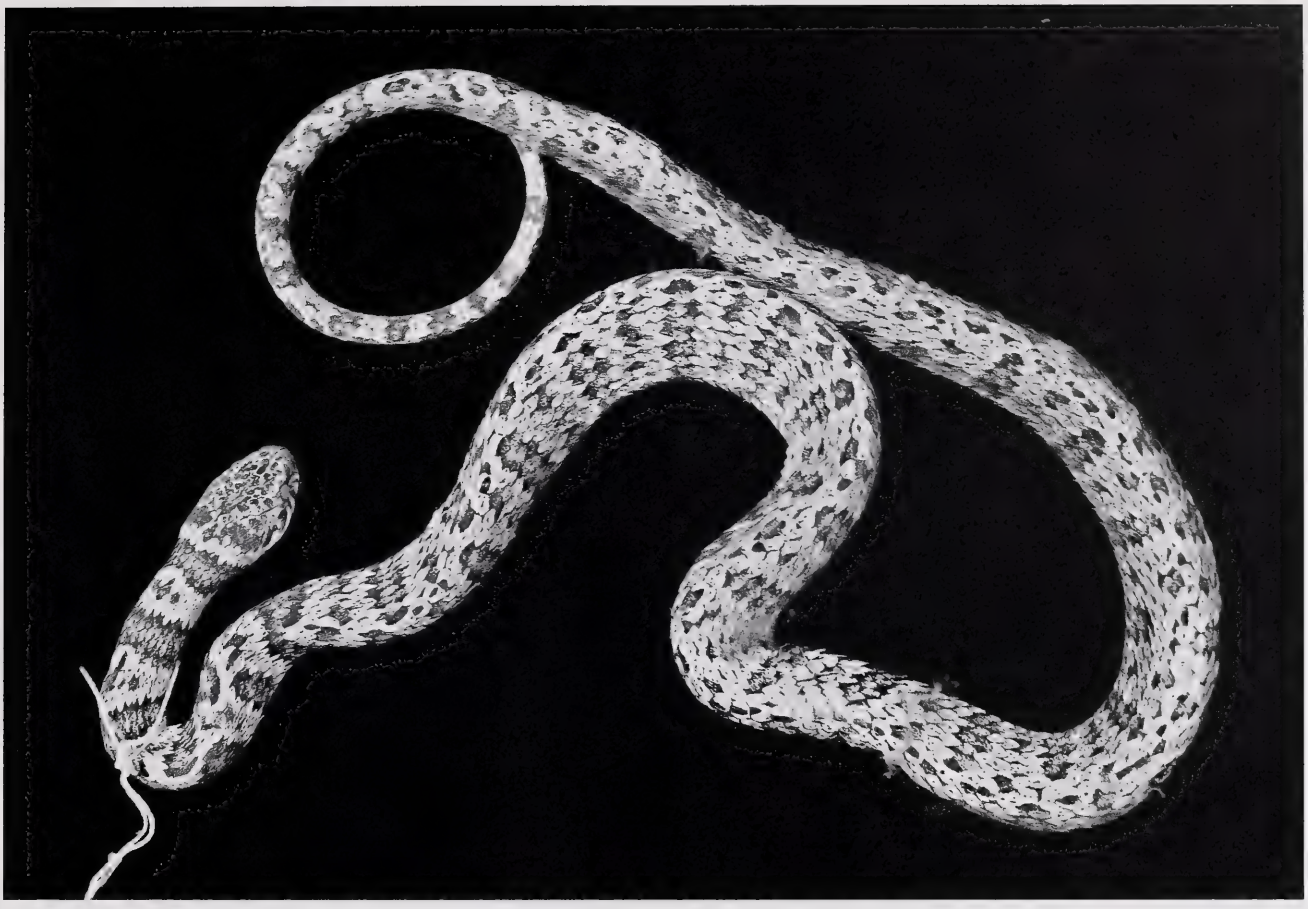

Figure 13. *Dipsas elegans* (Boulenger), an adult from Pallatanga, Chimborazo Province, Ecuador. This specimen represents the southernmost record for *D. elegans.* Boulenger (1896: 454) referred this specimen to "*Leptognathus mikanii,* variant C," which he considered equivalent to "*Leptognathus oreas* Cope."

lipsifera): "The ecological conditions are similar to those of the places inhabited by [*Dipsas ellipsifera*] but there are notable exceptions, for example Chiriboga [Pichincha Province] . . . has a very rainy climate and is covered with dense vegetation (according to the Holdridge Classification: Very Humid Lower Montane Forest), which in part has been destroyed through charcoal production." This characterization could well apply to higher elevation localities in the rain shadow valley of the upper Río Guayallabamba (Cumbayá, El Quinche, Tumbaco). However, many of the localities at lower elevations are in the area of western Ecuador that formerly was covered with primary lowland and lower montane rain forests before their major destruction during the last century (Chapman, 1926; Dodson and Gentry, 1991). It seems likely that these ecosystems were primary ones for *D. elegans.*

Orcés and Almendáriz (1987) reported a clutch of seven eggs of *Dipsas elegans* found in humid soil underneath decomposing logs in August 1987 at Chiriboga (Pichincha Province), Ecuador (Fig. 8: locality 12).

Dipsas oreas (Cope) Figures 8, 14–23

Leptognathus oreas Cope, 1868: 109. Type locality: "the elevated Valley of Quito" (here inferred to be southern Ecuador; see discussion below). Holotype: ANSP 10115 (original number 6707 given in Cope's description, possibly the Orton expedition field number).

Leptognathus mikani, part: Günther, 1872: 29; 1885–1902: 141. Boulenger, 1896: 453, 454 (variant C, specimens *a, b* from "W. Ecuador"; =BMNH 60.6.16.56, 60.6.16.63; see Figs. 14, 22). Despax, 1911: 36.

Leptognathus andrei: Boulenger, 1896: 453. Kofron, 1982: 50.
Sibynomorphus mikanii oreas: Amaral, 1929a: 31; "1929"b [1930]: 198.
Dipsas mikanii oreas: Parker, 1934: 271; 1938: 444 [misidentifications] (at least in part =*Sibynomorphus petersi* and *S. oligozonatus*; Cadle, unpublished data).
Dipsas oreas: Peters, 1960a: 92. Miyata, 1982: 16.
Leptognathus andiana: Peters, 1960a: 92; 1965: 6. Resurrected from synonymy by Cadle and Myers (2003).
Sibynomorphus andianus: Peters, 1960a: 92.
Dipsas oreas elegans: Orcés and Almendáriz, 1987: 141. Pérez-Santos and Moreno, 1991: 154. Resurrected from synonymy herein.
Dipsas oreas ellipsifera: Orcés and Almendáriz, 1987: 141. Pérez-Santos and Moreno, 1991: 156. Resurrected from synonymy herein.

Notes on the Holotype

The holotype (ANSP 10115; see photograph in Kofron, 1982: fig. 2) is an adult male in relatively good condition (somewhat soft and with the jaws dissected). Basic data are the following, with differences from Cope's (1868) description indicated in parentheses: Total length, 691 mm (26 inches [=660 mm]). Tail length, 182 mm. SVL = 509 mm. Tail as a proportion of total length, 26%. Dorsal scales in ?-15-15 rows (anterior body damaged). Vertebral row slightly wider than paravertebral rows. Ventrals, 178 (180). Subcaudals, 82 (90). Anal scale single. Preoculars, 0/0 (prefrontal and loreal bordering the anterior edge of the eye). Postoculars, 2/2. Temporals, 1 + 3/1 + 2. Loreal pattern 2/2 (prefrontal and loreal bordering eye). Supralabials, 7/7 with 3–5 touching the eye on each side. Infralabials, 11/11; one pair of infralabials in contact behind the mental scale. Three pairs of subequal squarish chin shields. The maxillary tooth count could not be done because the jaws are dissected and somewhat damaged.

Dorsal bands on body 23, those on the anterior half of the body complete middorsally; posterior bands are interrupted middorsally and moderately to greatly offset. Anterior bands tend to have squarish or angular edges, whereas posterior bands are more elliptical. All bands have some evidence of pale centers. Cope (1868) commented that the venter of the holotype was "largely obscured with black," but much of the venter is white (see Kofron, 1982: fig. 2). In an accompanying key, Cope used the alternative and more accurate phraseology "belly much black spotted" (Cope, 1868: 108). The black markings on the venter are squarish, and many are aligned to form longitudinal arrays.

Diagnosis

Dipsas oreas is characterized by a moderate number of ventrals (167–184) and subcaudals (males, 82–91; females, 70–83) and a low number of maxillary teeth (12–14). It is a grayish to brownish snake with distinct bands and/or blotches that extend ventrally to the lateral edges of the ventral scales (Fig. 14). At least one, but usually more, complete bands are present on the anterior body, but posteriorly the bands tend to break up into a series of lateral blotches (often offset). The anterior bands are usually squarish, longer than tall, and broader than the interspaces; posterior bands are narrowed, sometimes reduced to vertical bars, and much narrower than the interspaces. In adults the centers of the bands are lighter than peripheral portions, but the lightening is never so extensive as to produce immaculate centers (i.e., scales in the central portions always retain dark flecks or spots). In a few specimens, most of the central portions of the bands is lightened so that the bands are distinguished by their darkened borders only (see Fig. 19). In this regard, Peters' (1960a: 33, 1960b: 515) "key" character that the bands in *D. oreas* are "never so light that the [bands] resemble paired ellipses" is occasionally violated. Nonetheless, the bands in *D. oreas* never attain the form of those in *D. elegans* or *D. ellipsifera*, in which the central parts of the bands are sometimes immaculate white. In small juvenile *D. oreas*, the bands are solid (without pale centers), and some adults are relatively unicolored posteriorly (Figs. 15, 19).

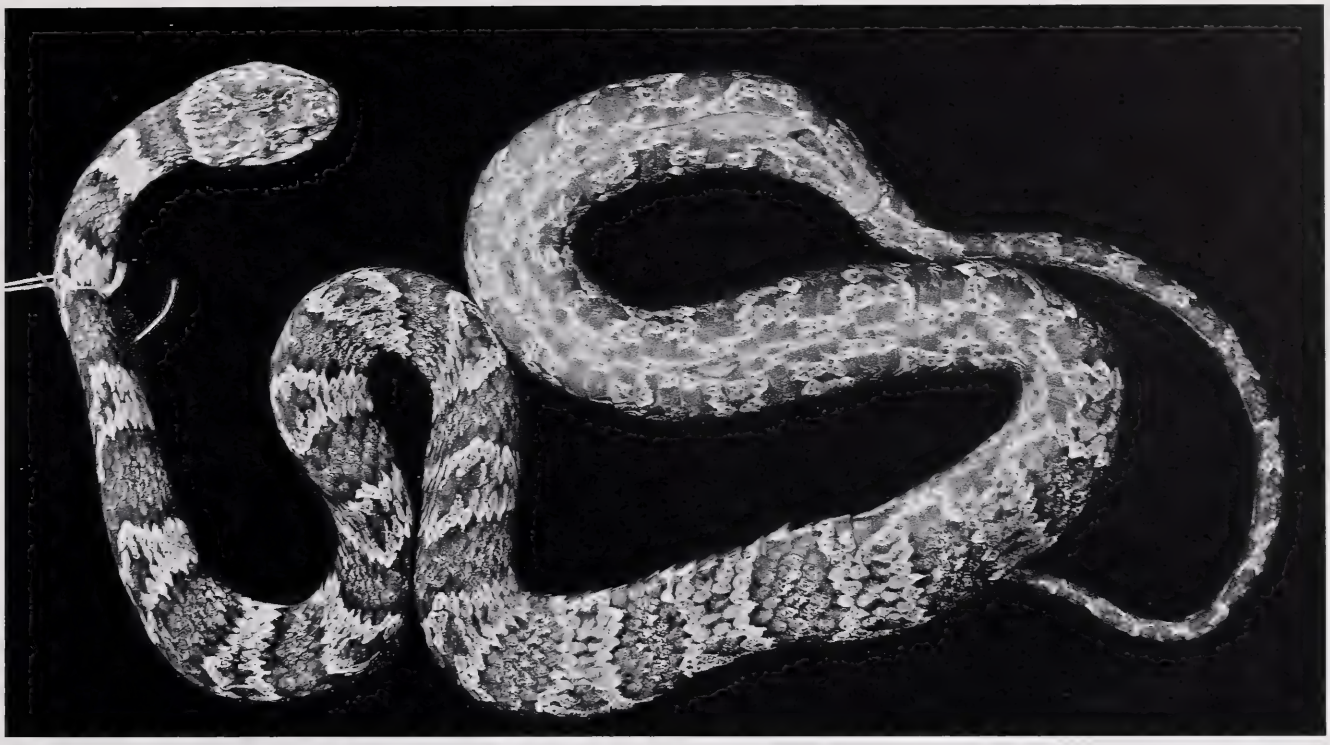

Figure 14. *Dipsas oreas* (Cope). Specimen from an unknown locality in western Ecuador showing a typical dorsal and posterior ventral pattern (BMNH 60.6.16.56; see Fig. 22 for detail of head). Ecuadorian specimens of *D. oreas* have narrower anterior bands than Peruvian specimens (compare Figs. 18, 19).

The top of the head in *Dipsas oreas* usually has an elongate blotch with irregular edges centered on each parietal scale and much additional irregular spotting or darkened suture lines on the head (see Fig. 20). The venter is usually strongly patterned with light and/or dark spots or squarish blotches, sometimes a checkerboard pattern or spots aligned in longitudinal arrays. See additional discussion and photos in Cadle and Myers (2003: 21–25).

Dipsas oreas is distinguished from other species of *Dipsas* in western Ecuador as follows. *Dipsas ellipsifera* has fewer ventrals (153–164) and subcaudals (62–78) and has a color pattern consisting of narrow vertical bands or bars with light (whitish) centers. *Dipsas elegans* has broadly overlapping scale counts with *D. oreas* (except male subcaudal counts; see Table 1) but has narrow vertical bands or bars with distinctly light (usually pale brown) centers (compared with the more subtle lightening in *D. oreas*), more maxillary teeth (17–21), and a different pattern of scales in the loreal region (see Table 1). *Dipsas oreas* has a high frequency of the preocular scale fused with the prefrontal, a rare condition in *D. elegans*.

Dipsas andiana has a distinctive U- or V-shaped marking on the top of the head and high numbers of ventrals (≥185) and subcaudals (≥91 in males, ≥80 in females; Cadle and Myers, 2003). *Dipsas gracilis* and *D. temporalis* differ from *D. oreas* in having very broad bands that are much wider than interspaces the entire length of the body, the anterior bands encroaching broadly onto the ventral scutes or complete across the venter, and high ventral counts (187–210 in *D. gracilis*; 187–208 in *D. temporalis*) and subcaudal counts (94–128 in *D. gracilis*; 119–132 in *D. temporalis*). (Data for *D. temporalis* include upper ranges reported in Peters, 1960a).

As discussed in the species account for *Dipsas elegans,* the greatest difficulty is in distinguishing small juveniles of *D. oreas* and *D. elegans* because both have solid blackish bands without pale centers (Figs.

11, 12, 17). *Dipsas oreas* tends to have fewer bands than *D. elegans*. This character, in combination with others, is decisive in species determinations. For example, ANSP 18123 has a somewhat atypical head pattern and high number of body bands (30) for *D. oreas*. However, other characteristics of ANSP 18123 are typical of *D. oreas* and quite unlike *D. elegans*: it has a low number of maxillary teeth (13) and loreal pattern 1 typical of *D. oreas* (pattern 3 or, rarely, pattern 4 in *D. elegans*; Fig. 1).

Apart from *Dipsas oreas*, the only other species of *Dipsas* definitely known from west of the continental divide in Peru is *D. gracilis*, which was recently reported from Tumbes department (Tello, 1998) and possibly occurs in Piura department as well. Another species, *D. latifasciata*, is known from immediately west of the continental divide in northern Cajamarca department. *Dipsas latifasciata* generally has more ventrals (179–194) and subcaudals (91–111) than *D. oreas* and more maxillary teeth (16–19), and the top of the head in *D. latifasciata* is generally solid black or with fine pale reticulations on a predominantly dark background. Notes on the distribution and taxonomy of *D. gracilis* and *D. latifasciata* are given later in this report.

Description

The following description of *D. oreas* is based on variation summarized in Table 1, which gives additional details.

Size, Scutellation and Dentition. The largest specimen examined was a male 758 mm total length, 543 mm SVL. The largest female I examined was 732 mm total length, 566 mm SVL. However, Kofron (1982: 49) reported that the holotype of *Leptognathus andrei* Sauvage, a synonym of *Dipsas oreas*, was a female 827 mm total length, 626 mm SVL. Tail 25–28% of total length in males, 21–24% in females. Body strongly compressed. Dorsal scales typically in 15-15-15 rows, although other patterns occur (Table 1). Vertebral scale row slightly wider than, to 1.5× the width of paravertebral rows in adults, but relatively wider in juveniles. Ventrals 167–184 (averaging 176) in males, 167–181 (averaging 176) in females; hence, there is no sexual dimorphism in ventral counts. One to 3 preventrals anterior to ventral series (see Myers, 2003, for discussion). Subcaudals 82–91 (averaging 87) in males, 70–83 (averaging 76) in females. Total segmental counts 251–271 in males, 241–263 in females. Scales in the loreal region highly variable; often, both a loreal and a preocular border the anterior edge of the eye, but the preocular is frequently fused with the prefrontal and either the loreal or the preocular may be further divided. Loreal pattern typically 1 or 2, but high frequencies of patterns 5 and 6 occur, particularly in Peruvian specimens (Table 1, Fig. 1; see later discussion of geographic trends). Head scales variable: postoculars usually 2 or 3 (occasionally 1 or 4), primary temporals usually 1, 2, or 3 (rarely 4), secondary temporals usually 3 or 4 (range 2–4), supralabials 6–9, usually with supralabials 4–5, 3–5, or 4–6 bordering the eye, but these patterns are highly variable (Table 1). Infralabials 9–13 (usually 11 or 12 in Ecuadorian specimens, 12 or 13 in Peruvian specimens). Either one pair ($N = 23$) or two pairs ($N = 6$) of infralabials in contact behind the mental or one infralabial contacts two on the opposite side ($N = 9$); the frequency varies geographically, as discussed below. Two or three pairs of squarish, subequal chin shields; if only two pairs of chin shields are present, these are usually followed by one or two pairs of gular scales that are longer than wide. Maxillary teeth 12–14 ($N = 23$).

Dipsas oreas shows minimal sexual dimorphism in some characteristics that are commonly sexually dimorphic within colubrids. Males have only slightly longer tails than females when the total sample is considered, and there are no significant differences in ventral numbers between the sexes (Table 1). However, within the population sample from the Río Zaña Study Site, males have significantly longer tails

than females (no difference in ventral number). Males average significantly greater subcaudal counts than females for both the "total" and "population" samples (Tables 1, 3). Females apparently attain greater body sizes than males in *D. oreas* (Table 1), but in the sample from the Río Zaña Study Site, the largest male and female were approximately the same SVL (Table 3). In the population from the Río Zaña Study Site, males and females apparently differ in the extent and manner of color change during growth (see next section).

Coloration in Life. Characteristic elements of color pattern in *Dipsas oreas* include (1) dark brown to black bands (wider than interspaces anteriorly, narrower posteriorly) on a grayish to pale brown ground color (bands usually broken into a series of lateral blotches on the posterior body), (2) a cephalic pattern usually involving a pair of large dark ovals centered on the parietal region and many other irregular dark markings, and (3) a venter that is usually dirty whitish with many dark squarish blotches (Figs. 14–19). The dorsal bands develop pale centers in larger snakes, the pale areas occasionally becoming so extensive as to obliterate most indications of bands (which remain as dark ellipses, the former edges of the bands). Some indication of bands was evident in all specimens examined, although bands are obscure in some large specimens (Fig. 19, bottom) because they nearly match the ground color. In these specimens, the bands are usually outlined with dark brown borders, and the anterior ones are usually more distinct than the posterior ones.

Except for brief notes (Cadle and Myers, 2003) no descriptions of coloration in life have been reported for *Dipsas oreas*. A specimen from southern Ecuador, KU 142803 (Cadle and Myers 2003: fig. 10), was described thus: "Dorsum tan with reddish brown blotches narrowly outlined with black. Venter cream with reddish brown spots. Iris tan" (field notes of Linda Trueb). In northern Peru, *D. oreas* shows considerable variation in coloration and pattern, and most variants can be found within a local area. Instances of extreme intrapopulational variation in color pattern are sometimes observed in other species of the tribe Dipsadini (e.g., Rossman and Kizirian, 1993). Nonetheless, the basic elements of the pattern are relatively constant in *D. oreas*. The variation is primarily due to greater or lesser emphasis on particular features of the pattern in different individuals. It is unclear whether such variation pertains to Ecuadorian populations because all Ecuadorian specimens examined have rather typical patterns in which the markings are rather bold. A moderately large sample of adults ($N = 10$) and juveniles ($N = 7$) from the Río Zaña Study Site makes it clear that ontogenetic change and, perhaps, sexual dimorphism account for some of the color variation in this species in northern Peru.

I herewith describe individual specimens from northern Peru to characterize some of the variation. I then describe the color pattern of a series of juveniles from the Río Zaña Study Site and discuss apparent patterns of ontogenetic change and sexual dimorphism. Color descriptions from life are taken from my field notes. Some of the pattern variants are illustrated in Figures 14–22; additional photographs of specimens of *Dipsas oreas* are found in Kofron (1982: fig. 2) and Cadle and Myers (2003: figs. 10, 11).

ANSP 31777 (Figs. 15, 19, 20; Río Zaña Study Site. Adult Female, 548 mm SVL). This is basically a brown snake with some obscure bands anteriorly, which fade posteriorly. The top of the head is medium brown with indistinct darker brown markings. Iris brown with lighter flecks. The upper labials are dull white, but heavily suffused, with medium brown concentrated along sutures and the upper parts of the scales. Lower labials are white with brown markings, but not so concentrated as on upper labials. Anterior 40% of body with broad brown bands that are most distinct anteriorly and fade posteriorly. Ground color between the bands is medium brown (as on the top of the head). Each band has darker brown anterior and posterior borders, with the band center about the same shade as the

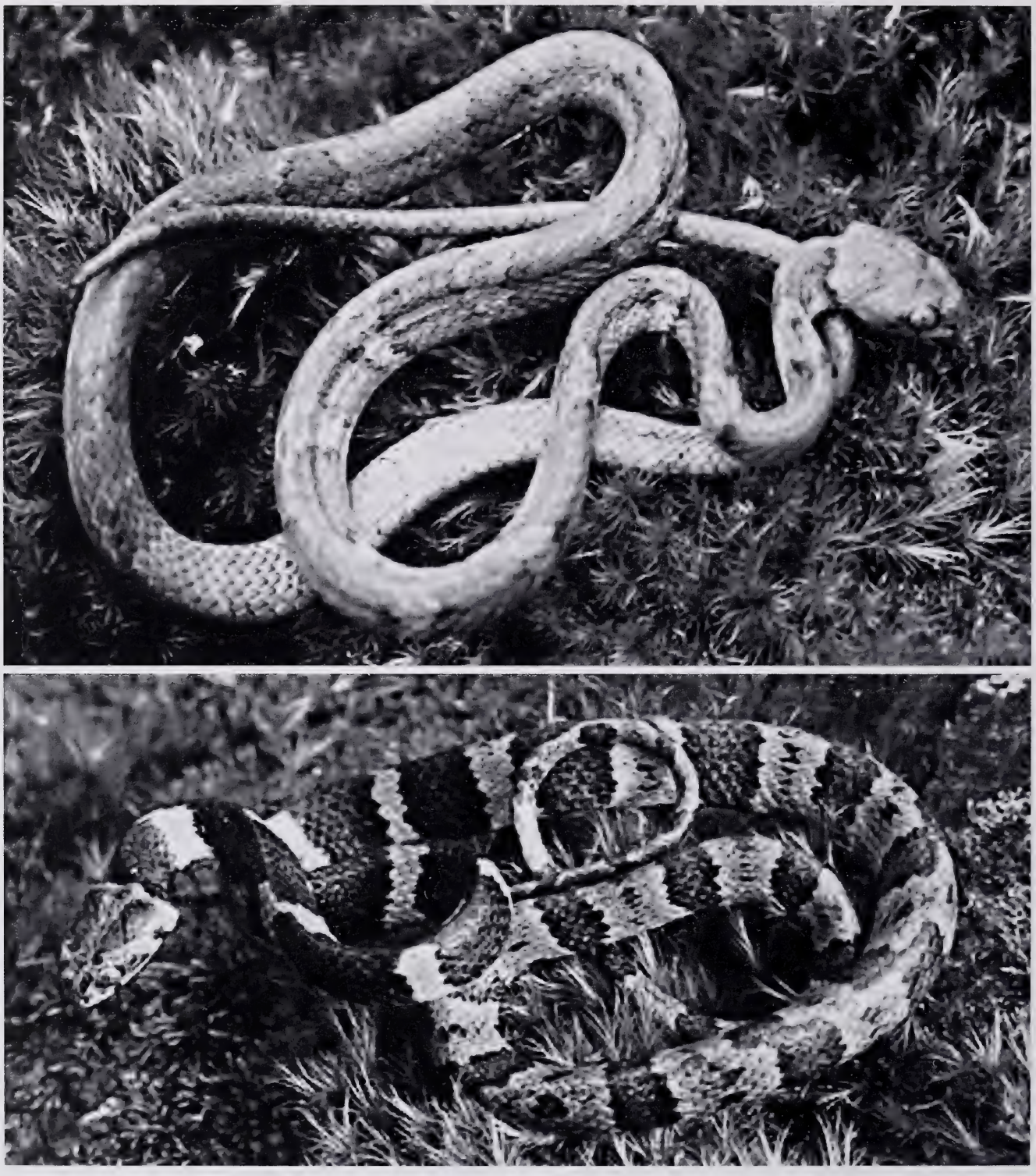

Figure 15. *Dipsas oreas* (Cope) in life from the Río Zaña Study Site (Cajamarca department, Peru). **Top:** a female with a dorsal pattern showing little contrast (ANSP 31777). **Bottom:** a male with a highly contrasting dorsal pattern (ANSP 31778). Note also the difference in the distinctness of the cephalic blotches (see Fig. 20). The male is in a defensive posture (Cadle and Myers, 2003: 36).

interspaces. The bands continue onto the lateral third of ventral plates. Posteriorly the bands become narrower and fade gradually, although they can be distinguished to the vent (the darker edges disappear after the first 10 bands). The tail is uniform medium brown. The venter is dull whitish but flecked heavily by grayish brown, flecking increasing posteriorly.

MUSM 5533 (Río Zaña Study Site. Adult Male, 472 mm SVL). The color is essentially as in ANSP

Figure 16. *Dipsas oreas* (Cope) in life from northern Piura department, Peru (MUSM 16750). An adult female with a highly contrasting anterior pattern, a much less distinct posterior pattern, and irregular cephalic blotches. The bands in this specimen are more irregular than most specimens from northern Peru.

31777 described above but the pattern is much more distinct. Interspaces between the dorsal bands are grayish brown, finely speckled with dark brown. Interspaces are much lighter than the center of the bands (compare ANSP 31777). Bands continue onto the tail, where about six can be distinguished. The bands tend to fade posteriorly, but they remain much more distinct than in ANSP 31777.

ANSP 31778 (Figs. 15, 18, 20; Río Zaña Study Site. Adult Male, 424 mm SVL). This individual is patterned much more boldly than other adults, and more similar to juveniles in the distinctness of the pattern. Interspaces light grayish brown. A series of black bands begins on the nape. The bands tend to have lighter (brown) centers, but this is not distinct except posteriorly. Bands extend onto outer third of ventral plates. Interspaces on the posterior half of the body are hatched with black, tending to form broken vertical bars. The top of the head is grayish brown with heavy black marking on most scales. Large black ovals cover the parietals and small posterior head scales. Iris grayish brown. Upper and lower labials grayish white, flecked with black. Belly whitish, stippled with dark brown, the stippling becoming heavier posteriorly. Underside of tail white but heavily stippled with dark brown.

MUSM 16750 (Fig. 16; Piura Department, Peru. Adult Female; 326 mm SVL). The dorsal ground color is medium brown with darker brown bands. The contrast between the ground color and band color is strongest anteriorly and weak posteriorly, where the bands are indistinct because their color nearly matches the ground colors. The anterior bands are much broader than posterior ones and are irregularly bordered by dark brown; posterior bands are narrow (2–3 scale rows) and not bordered by darker pigment except as isolated flecks. The five anterior bands are complete across the vertebral region; the remainder occur as a series of lateral blotches. Twenty-three bands on left side, 25 on right, between head and vent. The top of head is brown with dark brown irregular flecks. A pair of broad dark brown (partially bordered with black) arcs on parietals. Iris brown. Upper labials whitish, suffused with brown dorsally and with some dark pigment along sutures. Lower labials, throat, and anterior belly whitish. Brown pigment

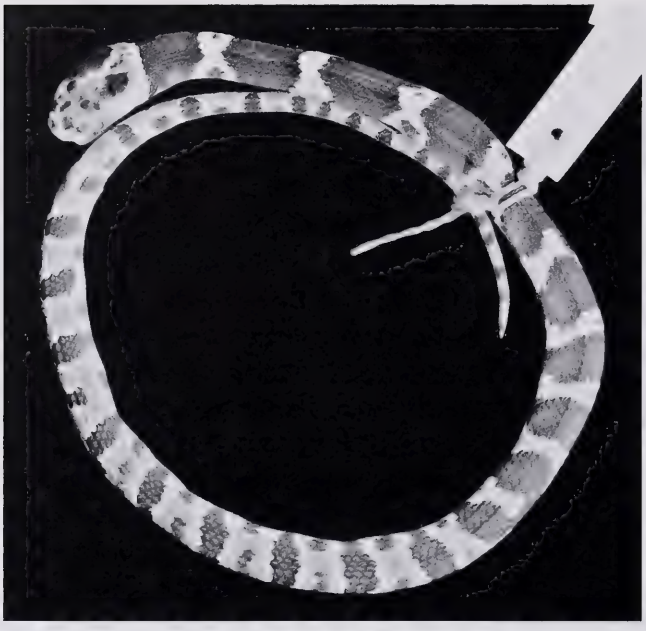

Figure 17. *Dipsas oreas* (Cope). A juvenile, solidly banded specimen from northern Peru (FMNH 232571, 163 mm SVL). Cadle and Myers (2003: fig. 11) illustrated two other juveniles.

increases posteriorly on belly, manifested by general darkening of ventral scutes. In addition, a series of brown (often white-bordered) bars is at the lateral edge of most belly plates. Small irregular ventrolateral markings are present on the outer edges of the ventral scutes, and lower dorsals often intercalated between dorsal (and lateral) bands. Tail coloration as in preceding body color.

FMNH 232570–72, MUSM 16751–52 (Fig. 17; Río Zaña Study Site. Hatchlings). Dorsum with broad black bands anteriorly, but narrower beginning at a point one-third to half way along the body. Bands tend to be offset posteriorly. Interspaces anteriorly are narrower than the bands, dirty white along the flanks, grayish brown with black pigment middorsally. Posterior interspaces are wider than the bands, grayish brown (somewhat lighter adjacent to bands), and with irregular black markings. In the posterior interspaces, and alternating with the bands, is a series of irregular squarish black blotches occupying the lateral edges of ventral scutes and part of scale row 1; there is one of these on each side per interspace. Top of head brown with irregular black pigment, mostly on parietals, prefrontals, and nasals. The elongate dark blotches characteristic of *oreas* are present in all specimens, but they tend to be somewhat more diffuse and fragmented than in many adults. The iris is grayish brown. Upper labials dirty white with a vertical black bar below the eye. Gular region dull white with some black spots on chin shields and anterior ventrals. Venter gray to brown, darker posteriorly, and irregularly peppered with tiny dark spots. Ventral surface of tail like posterior ventrals.

Ontogenetic Change and Sexual Dimorphism in Color and Pattern in Dipsas oreas. In contrast to the variation in color and pattern exhibited by adults of *Dipsas oreas,* hatchlings have a uniform pattern consisting of black bands and blotches on a white or gray ground color (Fig. 17; Cadle and Myers [2003: fig. 11] illustrate another hatchling from the same clutch of eggs). Most known hatchlings (i.e., specimens obtained from eggs hatched in the laboratory) are from the Río Zaña Study Site, the locality from which extensive color polymorphism in adults is documented. Other specimens within the size range of Río Zaña hatchlings or somewhat larger (e.g., ANSP 18120, 18123; MCZ 17083; UMMZ 56491; 150–193 mm SVL) all have solid bands. A still larger individual, USNM 98923 (292 mm SVL), has some evident lightening of the dorsal bands, as do all specimens with greater SVLs. Small juveniles and hatchlings of *D. oreas* of both sexes uniformly display similar color patterns, a contrast to adults.

Adult color patterns at the Río Zaña Study Site are highly variable. Some adults lose the highly contrasting pattern, whereas other individuals of comparable sizes retain contrasting patterns (Figs. 15, 18, 19). Adults that retain highly contrasting banding patterns are similar to juveniles except that the centers of the bands become lighter and the interspaces become more distinctly speckled with brown and/or black. Loss of highly contrasting dorsal coloration in some adults is apparently achieved by the interspaces and centers of the bands becoming invested with brown pigment, with only the borders of the bands retaining a much darker shade (blackish brown) than other parts of the dorsum (medium to light brown).

The differential expression of the pattern may be sexually dimorphic. The only two adult females from the Río Zaña Study Site (ANSP 31777, 31784; 548 and 551 mm SVL, respectively) are the largest individuals, and both lack highly contrasting dorsal colorations (Figs. 15, 19). Two adult

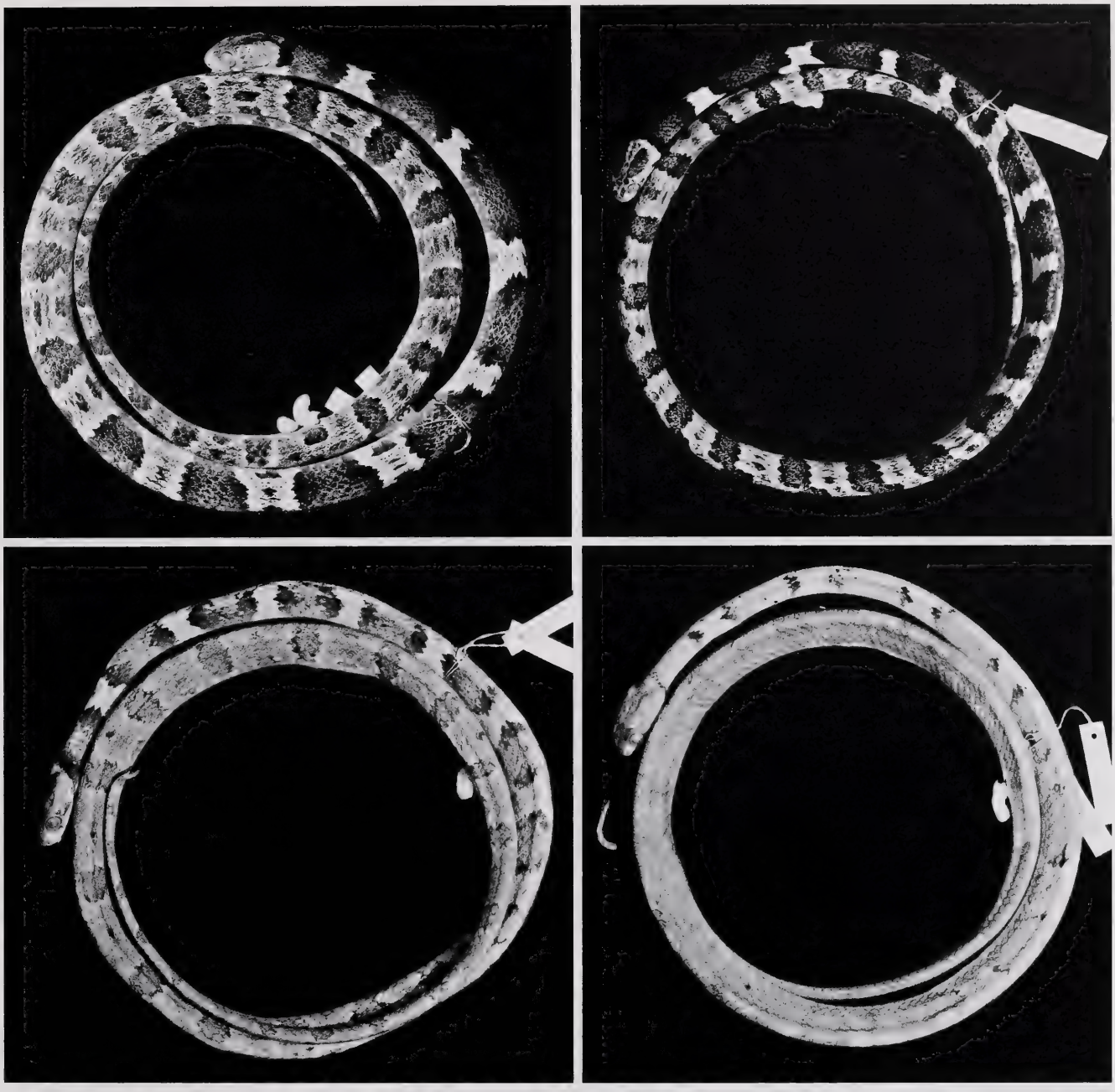

Figure 18. Variation in color pattern of adult male *Dipsas oreas* (Cope) from the Río Zaña Study Site (Cajamarca department, Peru). **Top:** left, ANSP 31779 (547 mm SVL); right, ANSP 31778 (424 mm SVL). **Bottom:** left, ANSP 31786 (543 mm SVL); right, ANSP 31780 (513 mm SVL).

males are of comparable sizes, but one (ANSP 31779; 547 mm SVL) retains a highly contrasting pattern, whereas the other (ANSP 31786; 543 mm SVL) is less contrasting but not as uniform as the two females (Fig. 18). Two smaller males (ANSP 31778, 31785; 424 and 506 mm SVL, respectively) retain highly contrasting patterns, whereas two others (ANSP 31780, 31783; 513 and 497 mm SVL, respectively) have reduced contrast (Fig. 18). A female (326 mm SVL) from another locality in northern Peru (MUSM 16750) has a highly contrasting pattern on the anterior body and much reduced contrast posteriorly (Fig. 16 and detailed color description above).

Thus, in the Río Zaña population, females possibly lose the highly contrasting juvenile patterns, whereas in males, the ex-

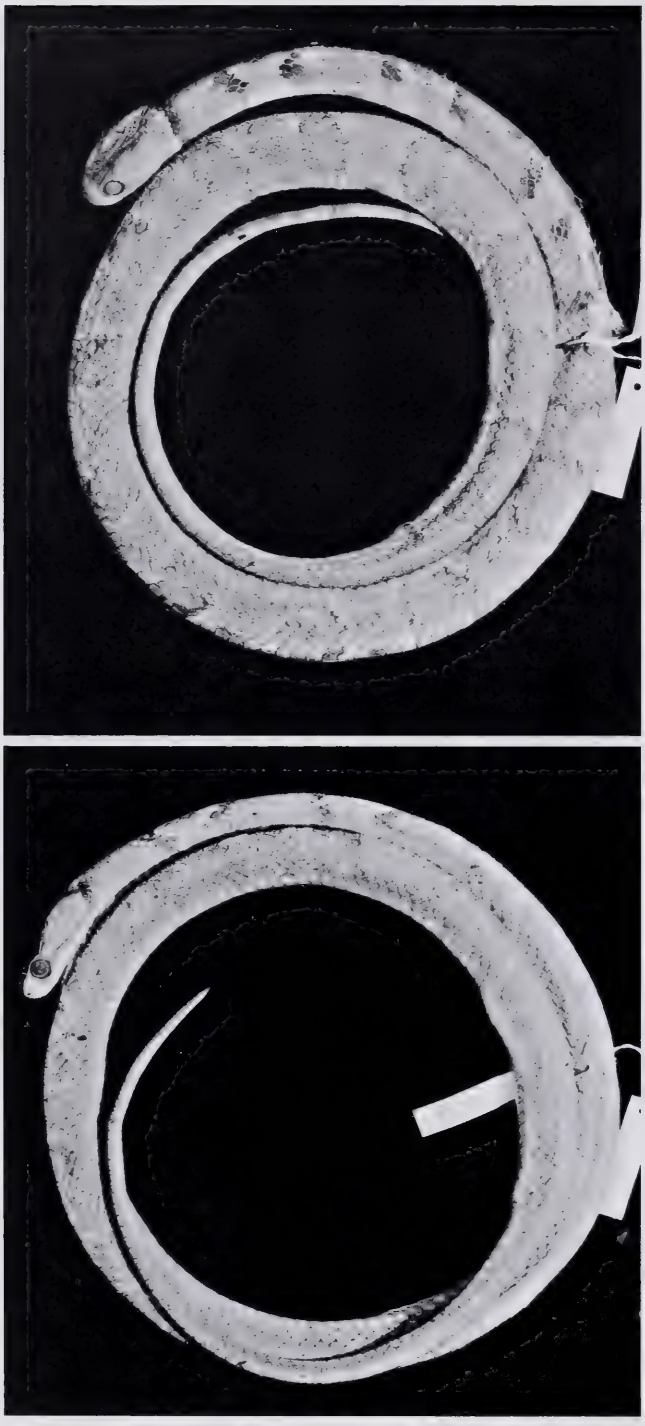

Figure 19. Variation in color pattern of adult female *Dipsas oreas* (Cope) from the Río Zaña Study Site (Cajamarca department, Peru). **Top:** ANSP 31777 (548 mm SVL). **Bottom:** ANSP 31784 (551 mm SVL).

pression of the contrast according to size is more variable. However, without larger samples and ontogenetic data on pattern changes, it is not possible to make definitive statements regarding sex or size differences in color pattern. It is also unclear whether the intrapopulational variation in color pattern at the Río Zaña Study Site applies to other populations. Sample sizes for different ontogenetic stages and sexes from single localities are insufficient to disentangle these effects from geographic or random variation patterns. Nonetheless, no examples of specimens with extremely pale bands or relatively unicolor dorsums are available from localities other than the Río Zaña Study Site.

Color and Pattern in Preservative. Preserved specimens retain the major pattern elements of live specimens, but colors become duller. Even specimens well over a century old (e.g., the holotype and BMNH 60.6.16.56; Fig. 14) have dark brown bands on a gray or grayish brown ground color. The lightening of the middle of the dark bands may become less evident in preservation, but most larger specimens retain even this sometimes subtle pattern characteristic.

Most specimens of *Dipsas oreas* have a pair of elongate oval blotches on top of the head from the level of the eyes to the nape (Fig. 20). These are more or less discrete, depending on how much additional black pigment occurs atop the head. Within the Río Zaña population, there is variation in the prominence of the blotches, just as in overall dorsal pattern (Fig. 20). Nonetheless, the characteristic form and presence of these cephalic blotches is a useful identifying characteristic for *D. oreas*. The lateral surface of the head is usually heavily and irregularly flecked with dark pigment, often concentrated along scale sutures and sometimes forming a more or less discrete diagonal postocular bar (Fig. 21).

Two specimens from unknown localities in western Ecuador, BMNH 60.6.16.56 and 60.6.16.63, have atypical head markings (Fig. 22). These lack distinct blotches on the parietals, although a pair of irregular blotches is evident on BMNH 60.6.16.56 that is similar to those on MUSM 16750 (Fig. 16). Instead, the top of the head is whitish but heavily marked with dark brown, resulting in a generally

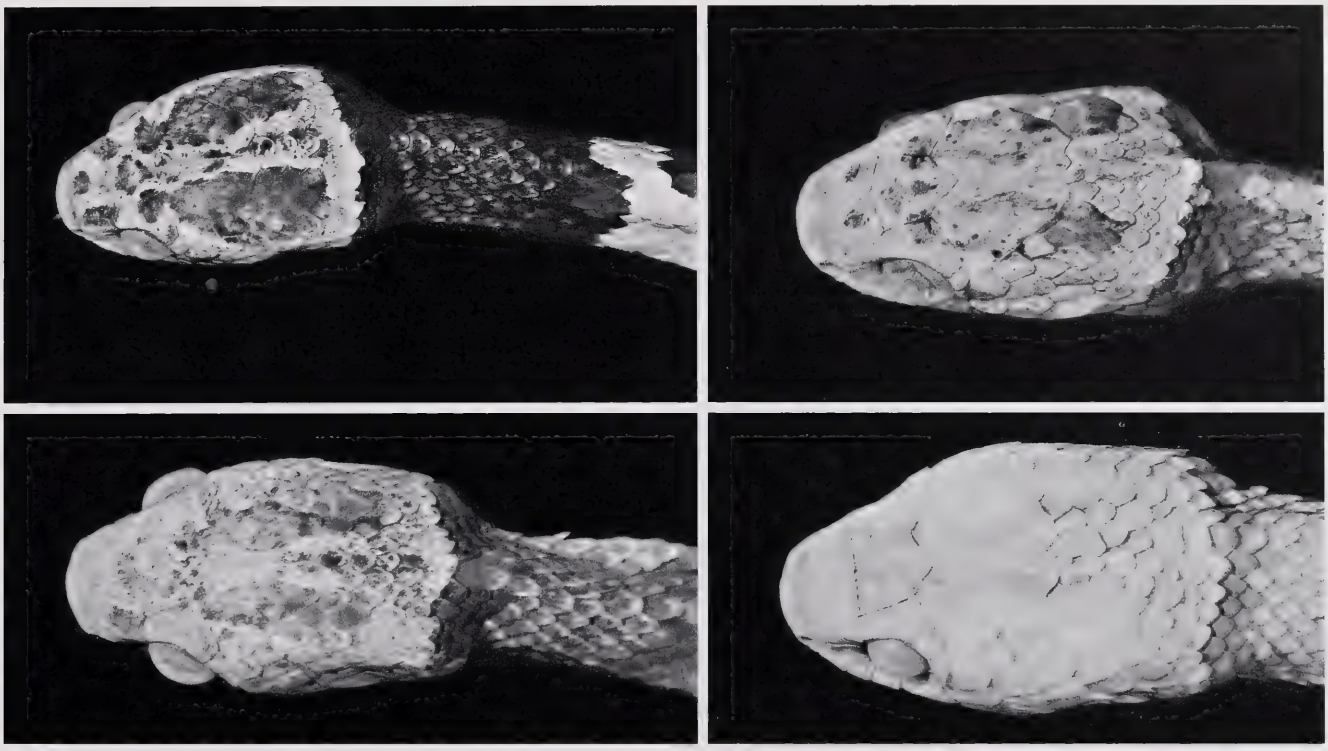

Figure 20. Variation in dorsal head patterns of *Dipsas oreas* (Cope) from the Río Zaña Study Site (Cajamarca department, Peru). **Top:** left, ANSP 31778 (male); right, ANSP 31786 (male). **Bottom:** left, ANSP 31779 (male); right, ANSP 31777 (female). The dark oval blotches centered on the parietal region are characteristic of most specimens of *D. oreas,* but vary within this population from very distinct to indistinct. In specimens that have very indistinct blotches (bottom right), at least the medial edges of the blotches are discernible by a dusky undulating border.

dark brown impression except under close inspection. The parietal scales of these specimens are irregularly marked with dark brown, which blends into the dark markings anteriorly and posteriorly on head. A few suture lines of the supra- and infralabials are marked with dark brown, especially anteriorly and posteriorly, but labial scales are rather unmarked compared with other specimens of *Dispas oreas.* Apart from the head patterns, the color patterns and other characters of BMNH 60.6.16.56 and 60.6.16.63 are typical of those seen in other specimens of *D. oreas* (Fig. 14).

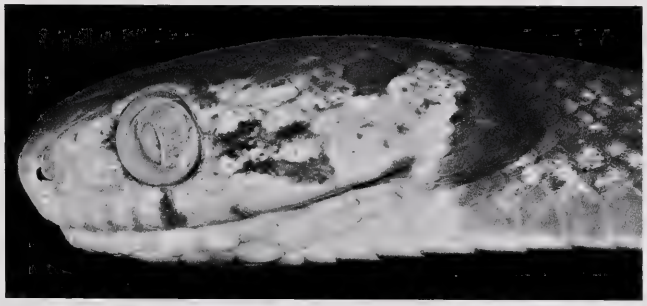

Figure 21. *Dipsas oreas* (Cope). Lateral view of the head of a specimen from the Río Zaña Study Site (Cajamarca department, Peru), ANSP 31785.

In a series of three specimens of *Dipsas oreas* from Chimborazo Province, Ecuador (ANSP 18117, 18120, 18123; adult female, juvenile female, and juvenile male, respectively), two show an obscure dorsal head cap without distinct parietal blotches, whereas the other (ANSP 18120; Cadle and Myers, 2003: fig. 11) has the parietal pattern typical of most *D. oreas.* In small juveniles, the parietal markings also tend to be more diffuse than in adults (Fig. 17 and above description of the coloration of hatchlings).

The venter of *Dipsas oreas* is usually moderately to heavily marked with large squarish spots or blotches, usually displaced toward the outer edges of the ventrals and sometimes aligned so as to form longitudinal arrays (Fig. 14). A few speci-

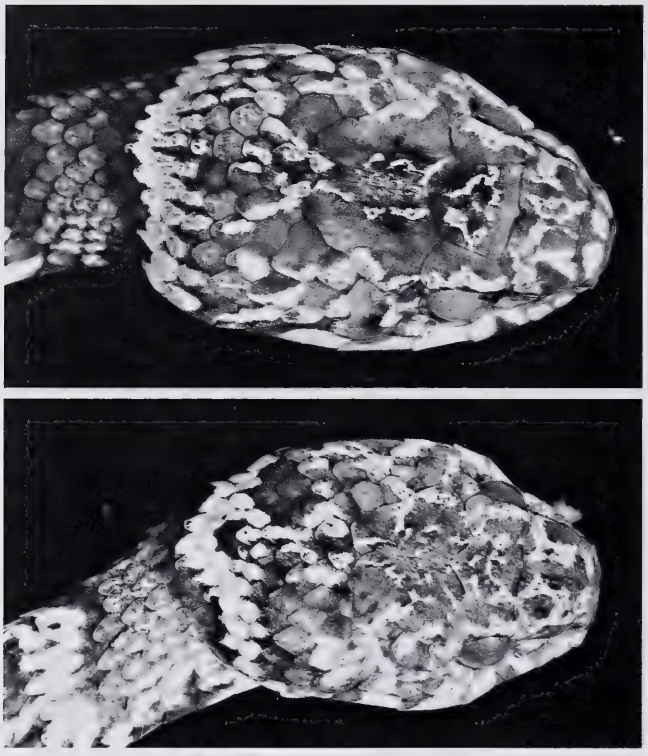

Figure 22. *Dipsas oreas* (Cope). Two specimens from unknown localities in western Ecuador with somewhat atypical head patterns. **Top:** BMNH 60.1.16.56 (see also Fig. 14). **Bottom:** BMNH 60.6.16.63. The cephalic blotches are less discrete in these specimens, in part because they are obscured by other irregular black and white mottling on the head.

mens (e.g., the holotype of *Leptognathus andrei* Sauvage illustrated by Kofron [1982: fig. 2]) have relatively unmarked venters.

Hemipenis

The following description of the everted hemipenis of *Dipsas oreas* is based on specimens from northwestern Peru (ANSP 31778–81, 31783, 31785–86; all field everted). The organ is fully capitate, and the capitulum is calyculate and very slightly bilobed distally. The calyces are surmounted by a dense array of fleshy papillae. With the exception of the most distal papillae, the tips of the papillae are spinulate (i.e., they have mineralized tips). The sulcus spermaticus divides at the base of the capitulum and has centrolineal branches that extend nearly to the center of each of the small lobes. A large nude pocket approximately one third the length of the organ is on the lateral surface of the organ, extending from the base to the encircling battery of spines around the midsection. The pocket is bordered by a thick lobe on each side. These lobes are ornamented with tiny spines, but otherwise, the basal portion of the organ on both the sulcate and asulcate sides is nude or with scattered minute spines.

The asulcate side of the organ has a pair of extremely large spines just distal to the basal nude portion, distally followed by a gap ornamented with tiny spines and then a dense battery of large, thick spines occupying the midsection just below the capitulum. This battery encircles the midsection of the hemipenis, ending on the sulcate side short of the sulcus spermaticus, which has smaller spines adjacent to it. There is some variation in the width of the asulcate battery of spines. In most specimens, the battery is about 3 spines across, but in one (ANSP 31781), the battery has only 2 rows of spines in most places and only 1 row in the middle of the asulcate side; another (ANSP 31780) has 4 rows of spines throughout most of the battery (tapering toward the sulcate side). The spines in the midsection have very thick bases, taper abruptly distally, and end with a short hook at the tip.

The relative proportions of one of the organs (ANSP 31779) are: total length, 16 mm; bilobed distally for approximately 1 mm. The capitulum occupies approximately the distal 5 mm on the asulcate surface. Sulcus spermaticus divided distally for about 8 mm. Length of basal nude pocket, 5.5 mm. The hemipenes of these Peruvian specimens of *Dipsas oreas* are similar in detail to the everted organs of a specimen from Loja Province, Ecuador (KU 142803). In KU 142803 there is, in addition, a large spine just distal to the nude pocket.

Geographic Variation in *Dipsas oreas* and the Identity of Peruvian Specimens

Dipsas oreas was previously documented in the Peruvian fauna in a brief note by Cadle and Chuna (1995: 32–33, footnotes

4, 5), who considered the species identification provisional at the time. Cadle and Myers (2003) discussed the species in resurrecting *D. andiana* from its synonymy; however, they did not specifically address the attribution of the Peruvian specimens to *D. oreas.* Some minor differences exist between the Peruvian and Ecuadorian specimens of *D. oreas,* but there is sufficient similarity to conclude that the range of *D. oreas* extends well into northern Peru. Nonetheless, some commentary concerning the referred Peruvian specimens is warranted. In assessing the following characterization of variation within Peruvian specimens of *D. oreas,* it is helpful to keep in mind that this sample is overwhelmingly dominated by specimens from the Río Zaña Study Site, which accounts for 17 of the 21 Peruvian specimens; thus, most of the variation within the "Peruvian sample" of this species actually represents intrapopulational variation within the Río Zaña Study Site population (Table 3).

There is a weak suggestion of a geographic cline in the number of dorsal bands on the body in *Dipsas oreas,* although samples are inadequate to analyze the trend thoroughly and are heavily weighted toward Peruvian specimens. Arrayed roughly north to south, the number of bands on the body in aggregated samples are (ranges followed by mean ± SD and sample size in parentheses):

Chimborazo Province + "Western Ecuador":
22–30, 24.8 ± 2.73 (N = 7)
Guayas Province, Ecuador:
23–29, 25.3 ± 2.21 (N = 7)
Loja Province, Ecuador:
19–30, 24.5 ± 7.78 (N = 2)
Peru:
17–24, 19.7 ± 1.63 (N = 19)

Differences in the number of bands for these samples is mainly accounted for by the width of bands on the anterior body, which generally cover 8–10 dorsal scale rows in Peruvian specimens compared with only 5–7 rows in Ecuadorian specimens. Midbody and posterior bands are of similar widths throughout the range (usually 3–5 scale rows).

Ecuadorian and Peruvian specimens of *Dipsas oreas* also differ in some scutellation and other characteristics, but these are primarily average or frequency differences rather than discrete character differences. The differences between the "Ecuador" and "Total" samples of *D. oreas* in Table 1 are accounted for by the incorporation of Peruvian specimens into the "Total" sample summary (see also Table 3 for summary characteristics of a population sample from Peru). Ecuadorian specimens average higher numbers of ventral scales; have different frequencies of loreal, temporal, and labial scale patterns; and differ in modal number of maxillary teeth. All Ecuadorian specimens (N = 18) examined have a single pair of infralabials in contact behind the mental, whereas Peruvian specimens (N = 19) have either a single pair (N = 7), two pairs (N = 4), or one infralabial contacting two on the opposite side (N = 8).

Loreal pattern 6 (Fig. 1) was observed only in specimens from the Río Zaña Study Site (Peru), but in this population it occurred with high frequency (13 of 40 observations, considering each side of a specimen as an independent observation). A few specimens do not fit the discrete loreal patterns outlined. For example, UMMZ 56491 (Chimborazo/Cañar Province, Ecuador) has, on the left side, a small preocular that lies superior to an extension of the prefrontal intercalated between the preocular and the loreal scale; the prefrontal touches the eye at little more than a point. The right side of the same specimen has loreal pattern 2, but a partial suture on the posterolateral portion of the prefrontal is suggestive of a partially formed preocular scale. Variations such as this, and the similar relationship between patterns 3 and 4, give credence to the idea of a developmental relationship between patterns 1 and 2 on one hand and patterns 3 and 4 on the other. These apparent developmen-

TABLE 3. SCALE COUNTS, MEASUREMENTS (MM), AND OTHER DATA FOR THE HOLOTYPES OF *DIPSAS OREAS* (COPE) AND *LEPTOGNATHUS ANDREI* SAUVAGE (= *D. OREAS*; DATA FROM KOFRON, 1982: 49–50) AND A POPULATION SAMPLE OF *D. OREAS* FROM PERU (RÍO ZAÑA STUDY SITE). SEE TABLE 1 FOR SEPARATELY TABULATED DATA FOR *D. OREAS* (ECUADORIAN SPECIMENS AND TOTAL SAMPLE). BILATERAL COUNTS FOR THE HOLOTYPES ARE SEPARATED BY A SOLIDUS (LEFT/RIGHT). DATA FOR THE RÍO ZAÑA SAMPLE ARE SUMMARIZED AS IN TABLE 1. *N* = NUMBER OF SPECIMENS OR OBSERVATIONS; SVL = SNOUT TO VENT LENGTH.

	Dipsas oreas holotype (ANSP 10115) Ecuador male	*Leptognathus andrei* holotype (MNHN 6285) Loja, Ecuador female	*Dipsas oreas* Peru (Cajamarca): Río Zaña study site
Total length (SVL) (mm)			
Largest male	691 (509)	—	758 (547)
Largest female	—	827 (626)	724 (551)
Tail length/total length			
Male	0.26	—	0.26–0.28 0.27 ± 0.008 (*N* = 10)
Female	—	0.24	0.21–0.24 0.23 ± 0.013 (*N* = 5)
Maxillary teeth	—	14	13 (*N* = 1) 14 (*N* = 7)
Dorsal scales	?-15-15	15-15-15	15-15-15 (*N* = 16) 15-17-15 (*N* = 1)
Ventrals			
Male	178	—	167–180 173.2 ± 4.39 (*N* = 12)
Female	—	178	167–178 172.0 ± 4.47 (*N* = 5)
Subcaudals			
Male	82	—	83–91 87.4 ± 2.50 (*N* = 11)
Female	—	79	70–81 75.6 ± 4.04 (*N* = 5)
Total segmental counts			
Male	260	—	251–271 (*N* = 14)
Female	—	257	241–259 (*N* = 5)
Anal scale	Single	Single	Single
Loreal pattern	2/2	2/2	2 (*N* = 20) 5 (*N* = 1) 6 (*N* = 13)
Preoculars	0/0	0/0	0 (*N* = 20) 1 (*N* = 14)

TABLE 3. CONTINUED.

	Dipsas oreas holotype (ANSP 10115) Ecuador male	*Leptognathus andrei* holotype (MNHN 6285) Loja, Ecuador female	*Dipsas oreas* Peru (Cajamarca): Río Zaña study site
Postoculars	2/2	3/2	1 (N = 3) 2 (N = 13) 3 (N = 18)
Primary temporals	1/1	1/1	1 (N = 2) 2 (N = 18) 3 (N = 13) 4 (N = 1)
Secondary temporals	3/2	3/3	2 (N = 1) 3 (N = 19) 4 (N = 14)
Supralabials (touching eye)	7(3–5)/7(3–5)	7(3–5)/7 (3–5)	6 (3–4) N = 1 7 (3–4) N = 1 7 (3–5) N = 9 7 (4–5) N = 8 8 (3–4) N = 1 8 (3–5) N = 2 8 (4–5) N = 9 8 (4–6) N = 3
Infralabials	11/11	9/10	10 (N = 1) 11 (N = 4) 12 (N = 16) 13 (N = 13)
Number of dorsal bands/ blotches on body[1]	23	About 31	17–22 19.7 ± 1.22 (N = 15)

Counts of body bands include only individuals having bands visible the entire body length.

tal relationships might explain a pattern of intraspecific variation in the *Dipsas oreas* group, whereby loreal patterns 1 and 2 or, alternatively, loreal patterns 3 and 4 tend to be characteristic of a species (Table 1).

All the scutellational differences and geographic trends are minor in view of the overwhelming similarities in both scutellation and color patterns between the Peruvian and Ecuadorian specimens of *Dipsas oreas.* However, the extensive variation in color pattern within and between populations of *D. oreas* in Peru (see discussion of color above) was not observed in specimens from Ecuador.

It is evident that the status of *Dipsas ellipsifera* and *D. elegans* relative to *D. oreas* has no bearing on the status of the populations of southern Ecuador and northern Peru here referred to *D. oreas.* All Peruvian specimens are referable to the nominotypical form of *D. oreas,* rather than to *D. ellipsifera* or *D. elegans,* as diagnosed herein. Orcés and Almendáriz (1987) noted that the range of "*D. oreas oreas*" extended farther south than the other subspecies but indicated that its distribution needed clarification. Their generalization appears to hold with the additional material examined for this study (Figs. 8, 23). *Dipsas ellipsifera* appears to be restricted to the Río Mira system of northern Ecuador, and I am unaware of specimens of *D. elegans* from south of central Ecuador (Fig. 8). In contrast, nominotypical *D. oreas* has previously been known south almost to the Peruvian border for more than a century (e.g., the holotype of *Leptognathus andrei* Sauvage from Loja). Hence, *D. elegans* and *D. ellipsifera* are not germane to evaluating the relationship of the Peruvian populations to nominotypical *D. oreas.*

Distribution and Type Locality

Dipsas oreas is distributed from approximately 2°10′S (southern Chimborazo Province, Ecuador) to the Río Zaña in Cajamarca Department, Peru (6°51′S; Figs. 8, 23). Because of a copying error, Cadle and Myers (2003:43, fig. 10) referred KU 142803 to Pichincha Province, Ecuador. The coordinates given for the locality are correct, but the province is Loja.

Most specimens of *Dipsas oreas* come from the foothills and slopes of the western cordillera of the Andes (elevational range 1,400–2,900 m). However, a true lowland locality is represented by a series (USNM 60006, 62797–02) from "Guayaquil, Ecuador (sea level)," a locality that seems out of character not only in terms of elevation but also in terms of habitats at other known localities for this species (see Chapman, 1926, and subsequent discussion of habitats). Cadle and Myers (2003) considered the records from Guayaquil "probably in error." I am no longer convinced that the locality is erroneous, but only that it seems different from other known localities. The series was obtained from Dr. Frederick W. Goding, American Consul General in Guayaquil, and was catalogued about 1920. Goding obtained specimens of other species known from western Ecuador for the USNM during the same period. Several specimens of *D. oreas* from imprecise localities in the Río Chanchan valley due east of Guayaquil (ANSP, MCZ, and UMMZ specimens) could be from <1,000 m elevation, and it is not possible to unequivocably rule out lowland localities for this species on the basis of present knowledge.

At the Río Zaña Study Site, the documented elevational range of *Dipsas oreas* is 1,450–1,800 m. From the distribution of appropriate habitats in this local area (as of 1993), the elevational range may be much greater (1,400–2,500 m). It is very likely that the distribution of *D. oreas* becomes increasingly restricted to mesic and humid environments on the Andean slopes toward the southern end of its range because the lowlands along the northern Peruvian coast are primarily occupied by arid to xeric habitats (Chapman, 1926; Koepcke, 1961). Nonetheless, small parcels of humid lowland tropical forests in Tumbes department could harbor populations of

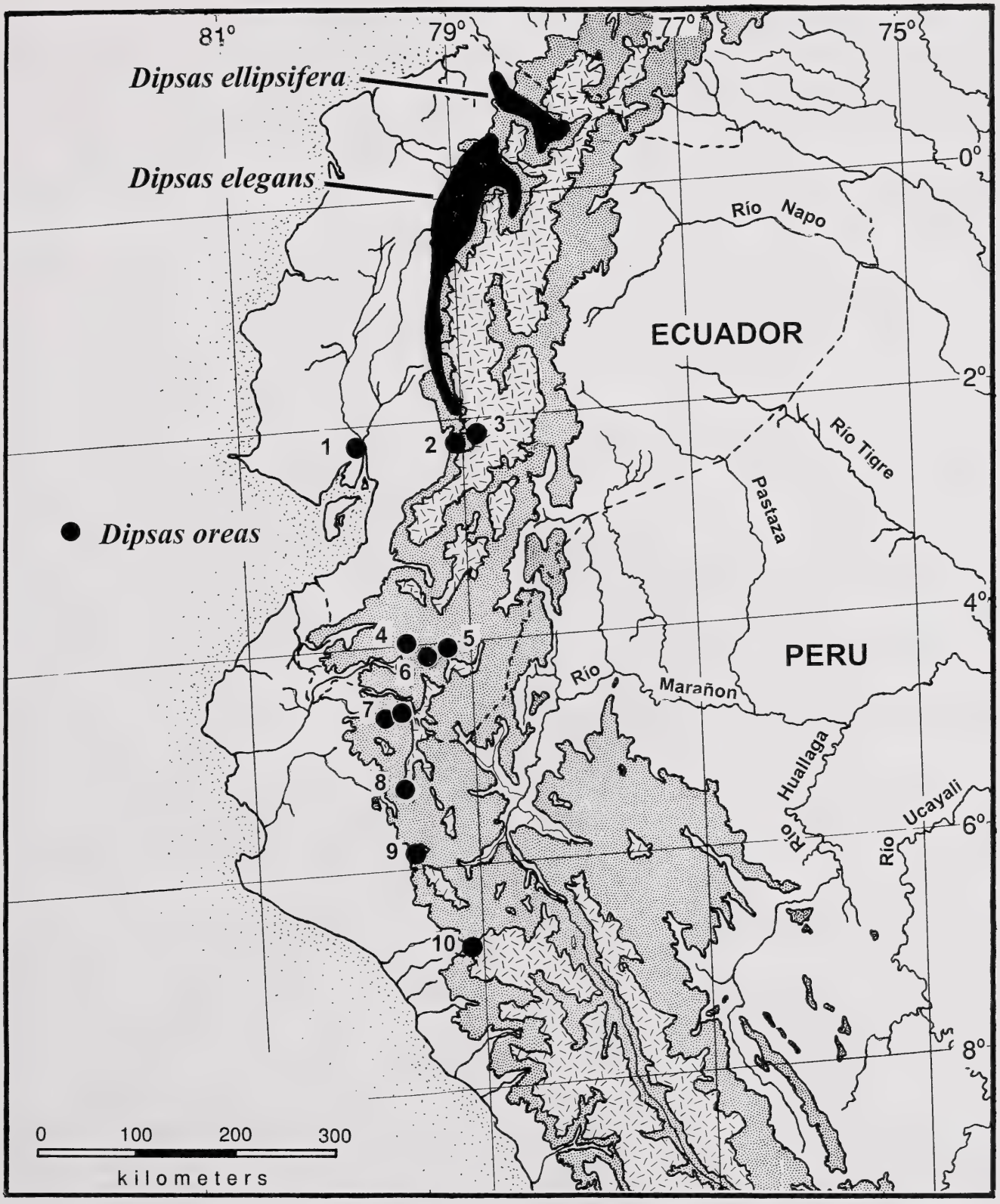

Figure 23. Ecuador and northwestern Peru showing summary distributions of *Dipsas ellipsifera* and *D. elegans* (based on locality records in Fig. 8), and locality records for *D. oreas* in Ecuador and northern Peru. Stippled area, above 1,000 m; hatched area, above 3,000 m. Numbered localities for *D. oreas* in Ecuador: **(1)** Guayaquil; **(2)** Huigra/Río Chiguancay and Río Chanchan valley; **(3)** Alausí; **(4)** Velacruz; **(5)** Loja; **(6)** Río Catamayo valley. In Peru: **(7)** Ayabaca and Cerro Aypate; **(8)** Canchaque; **(9)** Abra de Porculla; **(10)** Río Zaña Study Site.

D. oreas because another species, *D. gracilis,* has recently been discovered there (see later comments on *D. gracilis*).

Some known or suspected erroneous geographic records of *Dipsas oreas* in the literature bear some commentary. Parker's (1934: 271, 1938: 444) records of "*Dipsas mikanii oreas*" from the province of Loja in southern Ecuador seem to be based, at least in part, on misidentified specimens in the The Natural History Museum in London (BMNH) that I refer to *Sibynomorphus petersi* and *S. oligozonatus* (Cadle, unpublished data). Nonetheless, *D. oreas* is known from the province of Loja from other specimens (e.g., USNM 98923, KU 142803, and the holotype of *Leptognathus andrei* Sauvage). Fowler (1913: 169) referred three specimens to *D. ellipsifera* and *D. andiana* (ANSP 18117, 18120, 18123) that are here referred to *D. oreas* (Cadle and Myers, 2003: footnote 17, fig. 11). Peters' (1960a: 94, map 8) record of *D. oreas* from "Río Saloya" (Pichincha Province, Ecuador; Fig. 8: locality 7) is based on BMNH 1940.2.20.32, a juvenile here referred to *D. elegans.* Orcés and Almendáriz (1987: fig. 1) attributed the same locality to "*D. oreas oreas,*" probably based on Peters' record. Boulenger (1896: 454) referred four specimens to "*Leptognathus mikanii,* variant C (*L. oreas,* Cope)"; two of these (specimens *a* and *b,* BMNH 60.6.16.56, 60.6.16.63; Figs. 14, 22) from unknown localities in western Ecuador are *D. oreas,* but specimens *c* and *d* are *D. elegans* (see synonymy and distribution in the *D. elegans* species account).

On the other hand, Despax's (1911: 36) record of "*Leptognathus mikani*" from Alausí (upper reaches of the Río Chanchan valley, Chimborazo Province, Ecuador; Fig. 8: locality 17) probably correctly refers to *Dipsas oreas.* Despax (1911) stated that the specimen conformed to "Variant C" of Boulenger (1896: 454; ="*Leptognathus oreas*" Cope). In fact, Boulenger's "Variant C" included specimens of both *D. elegans* and *D. oreas* (see referred specimens in the synonymies given above for each species). However, *D. elegans* is not known from the region of Alausí, whereas *D. oreas* has been obtained by other collectors from the Río Chanchan valley (e.g., ANSP 18117, 18120, 18123; MCZ 17083; UMMZ 56491). Thus, it seems most likely that Despax's specimen is *D. oreas.*

With the above clarifications of literature records, it is clear that the northern limit of the distribution of *Dipsas oreas* is at approximately 2°S latitude. No confirmed records exist for *D. oreas* north of the Río Chanchan valley in southern Chimborazo Province. Additionally, there are no documented areas of range overlap for any of the three species of the *oreas* group (Fig. 8; contra Orcés and Almendáriz, 1987; Peters, 1960a). *Dipsas ellipsifera* seems likely to be restricted to the Río Mira basin and surrounding areas in northwestern Ecuador, whereas *D. elegans* is found to the south of that, along the western slopes of the Andes in northern and central Ecuador. Nonetheless, *D. elegans* is recorded from Pallatanga in the Río Chimbo valley (Chimborazo Province), the river system just north of the Río Chanchan valley from which *D. oreas* is known (Fig. 8: localities 14, 16, 17). The nearest localities for *D. elegans* and *D. oreas* (Pallatanga and Alausí, respectively) are separated by only about 26 km straightline distance (but also by a ridge >3,000 m). Thus, if there are areas of sympatry among any species of the *oreas* group, it seems most likely to occur between *D. elegans* and *D. oreas* in the region encompassing southern Bolívar/Chimborazo Provinces and adjacent areas of Guayas Province, Ecuador. Similarly, northern Imbabura Province (Fig. 8) is a potential area of contact between *D. elegans* and *D. ellipsifera.*

Most of the localities from which *Dipsas oreas* is documented are small remnants of once much more extensive humid forests (but see note below on a specimen from a dry semideciduous forest). In at least one instance, the locality near Porculla Pass

(Piura department, Peru) documented by MVZ 119330 (a road-killed specimen obtained in 1969), the population of *D. oreas* might be extinct. I visited the site in 1994 in an effort to sample remnant humid forests previously known to be extensive in this area (Koepcke, 1961). However, the easily accessible area had been completely denuded, except for a few trees remaining in steep ravines; a few small and highly fragmented forest remnants remain in this area (Sagástegui et al., "2003" [2004]). Most of the area is now very dry, and slopes are covered with grassland and occasional shrubs. I doubt that *D. oreas* and some other herpetofauna of humid montane forests of northwestern Peru (e.g., Cadle, 1989, 1991; Cadle and McDiarmid, 1990) can survive in such a habitat. The mid-1990s destruction of the forest of Monte Seco was mentioned above (see *Materials and Methods*). With continuing fragmentation and obliteration of these unique environments, endemics such as *D. oreas* will survive in increasingly smaller ranges or go extinct.

Curiously, despite the work of many herpetologists and other field biologists in western Ecuador, *Dipsas oreas* is known from relatively few specimens. Orcés and Almendáriz (1987) reported that the EPN collection contained no specimens, and Kofron (1982) stated that only eight specimens were known at that time. Recent brief biological surveys in southwestern Ecuador (e.g., Almendáriz and Carr, 1992) yielded no specimens of *D. oreas*. There is a distinct distributional gap between specimens collected in southern Chimborazo and Guayas Provinces (Río Chanchan valley and Guayaquil, respectively) and Loja Province to the south. However, few comprehensive collections are available from this area.

Clarification of the Type Locality: Orton's "Valley of Quito." James Orton was a naturalist and professor who obtained significant collections on several lengthy expeditions to South America, primarily Ecuador and Peru, in the 1860s and 1870s (Orton, 1875). Cadle (1989: 422–423) briefly summarized the Orton expeditions. The herpetological collections were turned over to Edward D. Cope of the Academy of Natural Sciences in Philadelphia, who catalogued the results of Orton's expeditions in a series of important papers on the herpetology of South America (Cope, 1868, 1874, 1876, 1877). Many species described by Cope (1868), such as *Dipsas oreas,* have the designated type locality "the elevated Valley of Quito," a vague statement that has been narrowly interpreted by most subsequent workers as the valley immediately surrounding the city of Quito, Ecuador (e.g., Peters, 1955: 347). Hence, "Valley of Quito" has often been questioned as a type locality for many reptiles described from Orton's collections because they are species unlikely to have ever occurred in that vicinity. However, Orton himself makes clear that his meaning was much broader, as noted by Orcés and Almendáriz (1987) and indicated in this quotation from Orton (1871: 620) and further amplified in his book (Orton, 1875: 152 ff.).

> The Valley of Quito . . . is a remarkably well-defined district, having a uniform temperate climate. It is nearly three hundred and fifty miles in length, stretching from 1°N. to 4°S., and has an average width of forty miles, being walled in by the grandest group of volcanic mountains in the world. These barriers have an average elevation of 12,000 feet above the sea, and are broken at few points, chiefly by the narrow gorges of the Santiago and Pastaza, and the sources of the Mira and Esmeraldos. The valley is subdivided by ridges into three basins—Quito, Ambato and Cuenca, having the respective altitudes of 9500, 8000 and 7500 feet. . . .

Thus, Orton's "Valley of Quito" comprised the entire Ecuadorian highlands from the Colombian border to the vicinity of Loja in southern Ecuador. The species described from this "locality," including *Dipsas oreas,* could have come from virtually anywhere in the Ecuadorian highlands or their western slopes. Cope (1868: 96) adds the following details, obtained directly from Orton, concerning the collections of 1867–68: "[The expedition] first

touched the continent at Payta, Peru [=Paita], and afterwards at Guayaquil; then proceeded inland over the Andes to Quito; thence [eastward to the Río Napo]. . . . They collected Reptiles chiefly from Guayaquil, Pallatanga (on the west slope of the western Cordillera south of Chimborazo); Ambato (in Valley of Quito); western slope of the volcano Antisana, 13000 ft. above sea (a small black frog). . . ." A similar route between Guayaquil and Quito was followed by later naturalists (e.g., Samuel N. Rhoads) and resulted in specimens of *D. oreas* (e.g., ANSP 18117, 18120, and 18123 obtained by Rhoads; MCZ 17083, UMMZ 56491). Fowler (1913: 153) says of the Rhoads collection that it ". . . was made on the western slope of the Andes, from Guayaquil to Quito. . . ." Thus, the Orton expedition of 1867–68 crossed that portion of southern Ecuador from which *D. oreas* is well known (Fig. 8) and followed a route commonly used in the 18th and early 19th centuries. The holotype of *D. oreas* was most likely obtained en route between Guayaquil and the upper slopes of the Cordillera Occidental directly to the east. Of the localities specifically mentioned by Cope (1868) and quoted above, *D. oreas* is known from subsequent collections at Guayaquil, but Pallatanga represents the southernmost locality for *D. elegans* (Fig. 8: locality 14), from which *D. oreas* is not documented.

Apart from species recorded from Guayaquil, virtually none of Orton's specimens from western Ecuador reported by Cope (1868) have locality data more precise than "Valley of Quito." In a curious paradox, Orton (1871: 619) began his paper with a lengthy discussion of the importance of accurate localities and the failure of previous field workers in Ecuador (e.g., Fraser) to supply accurate specimen data: ". . . we are still very far from knowing the precise range of species. This has arisen partly from the failure of collectors to give exact localities." Thus, although it is clear what Orton himself meant by "Valley of Quito," that understanding does not further elucidate the geographic origin of the species described from this type locality.

Natural History: Habitats, Seasonal Activity Patterns, Eggs, and Hatchlings

Habitats and Seasonal Activity Patterns. In northern Peru *Dipsas oreas* seems to be primarily an inhabitant of humid montane forests, although it occurs in secondary forest habitats if these are recent or adjacent to existing primary forests. MUSM 16750 was collected from an area of second growth at the base of Cerro Aypate (Piura department), which still had a fragment of humid forest on its crest in 1991 when the specimen was collected. Alwyn H. Gentry, who accompanied me to Cerro Aypate in 1991 classified the forest as "bmh-MT" (very humid montane forest) in the Holdridge Life Zone System (Gentry, 1995: "Cerro Aypate, Piura" in table 1). At the Río Zaña Study Site, *D. oreas* was collected from 1,450–1,800 m elevation and always inside or at the edge of primary montane humid forest. The lowest elevation constitutes the lower edge of the humid forest belt as it existed in 1987–90. Appropriate habitat at the Río Zaña Study Site occurred up to approximately 2,500 m, which might be the upper elevational extent for *D. oreas* in that local area.

During extensive field work in other areas of northern Peru, I did not encounter individuals in subhumid or arid habitats, which are common throughout the montane regions of northwestern Peru. However, a specimen from southern Ecuador was found "in a bromeliad, by day, in dry semi-deciduous thorn forest" (field notes of Linda Trueb for KU 142803). Thus, the habitat breadth of *Dipsas oreas* may be greater than suggested by my field experiences, which primarily derive from the Río Zaña Study Site. Nonetheless, all the known localities in northern Peru are areas in which fragments of humid montane forest are known to have occurred, at least historically (see *Specimens Examined and Locality Records* and Koepcke, 1961).

Wet and dry seasons at the Río Zaña

Study Site are very pronounced. Except for egg clutches found during the early dry season, I found *Dipsas oreas* only during the rainy season (approximately December or January to March or April) at the Río Zaña Study Site, although MUSM 16750 was collected 24 September 1991 at a site farther north. The contrast in activity pattern is best seen by comparing encounters during two field seasons at the Río Zaña Study Site. In nearly 2 months of continuous field work during May and June (early dry season), no *D. oreas* (except eggs) were encountered, whereas in only 2 weeks of field work from the same field camp in January (early rainy season), 10 adults and several juveniles were found. Few collecting dates accompany other specimens of *D. oreas*, but specimens have been obtained in July (KU 142803) and August (MVZ 119330). The climatic conditions that affect seasonal activity in *D. oreas* are probably very localized. The Río Zaña Study Site is the southernmost locality known for the species, and it is probably more strongly seasonal than localities farther north.

These observations suggest that *Dipsas oreas* is surface active at the Río Zaña Study Site only when ambient humidity is relatively high. During the dry season (roughly June to September), it may conceal itself in inaccessible retreats deep underground. Large boulder jumbles offering deep crevices and large surface boulders are common at the Río Zaña Study Site. Anecdotal observations (e.g., the propensity to dry out when kept in cloth bags in the field) suggest that, like some other species of *Dipsas*, *D. oreas* is particularly prone to desiccation (personal observations). This probably explains why no specimens were encountered during 2 months of field work during the early dry season. Temperature could also be a factor, for although average nocturnal (minimum) temperatures are only slightly higher in the rainy season compared with the dry season, the dry season was characterized by less night to night temperature equability and greater frequency of lower minimum temperatures than the wet season (see *Materials and Methods*). The rainy season also corresponds to the period when gastropod prey of *Dipsas* are most active on the surface (see next section).

Diel Activity Patterns, Diet, and Defensive Behavior. At the Río Zaña Study Site, *Dipsas oreas* is active nocturnally and encountered in saplings or shrubs. All active adults were found less than 2 m from the ground, and most were encountered on nights of high humidity or light rain. This species possibly never ascends to great heights in vegetation. Inactive individuals were encountered during the day on or below the surface of the ground in the following circumstances summarized from my field notes (all except MUSM 16750 from the Río Zaña Study Site).

ANSP 31779–81, 31783–86 (adult males and one adult female; see subsequent section on aggregation behavior): In well-shaded montane humid forest on the surface of leaf litter or beneath the surface litter at 1015 hr, 25 January 1989.

ANSP 31777 (adult female): Under a rock (40 cm diameter) in undisturbed montane humid forest at 1730 hr, 13 January 1989.

MUSM 5532 (near-hatchling, 178 mm SVL): Under a rock in the morning at the lower edge of the humid forest, 15 January 1989.

MUSM 16750 (adult female; Fig. 16): In a crevice in hardened lateritic soil during the day on 24 September 1991 (corresponding to the late dry season). The crevice was in a road cut in disturbed habitats at 1,950 m; it measured 2 cm wide at the ground surface, was >50 cm deep, and was covered by dead brush above. The snake was coiled about 4–5 cm below ground level and about 20 cm from the surface in a horizontal direction. The location within the crevice where the snake was found was quite dry, although it was much wetter deeper within the crevice.

In addition to these observations suggesting that *Dipsas oreas* retreats underground or under surface objects when inactive, several clutches of *D. oreas* eggs were found within a crevice in the ground at the Río Zaña Study Site (see *Eggs and Hatchlings*). On the other hand, a specimen from a dry thorn forest in southern Ecuador was found in a bromeliad (KU 142803).

Species of *Dipsas* are well known to prey upon terrestrial gastropods (e.g., Cunha and Nascimento, 1993; Martins and Oliveira, 1998; Peters, 1960a; Sazima, 1989). A single food record is available for *D. oreas* from the Río Zaña Study Site. The posterior portion of the intestine of ANSP 31777 was packed with slug and/or snail remains. Terrestrial and arboreal gastropods were both abundant and diverse at this locality during the rainy season.

Dipsas oreas exhibits defensive posturing common among species of Dipsadini (Cadle and Myers, 2003), including head triangulation, raising the anterior part of the body, and bringing the head and neck back into an S-shaped loop (Fig. 15). Individuals occasionally added an additional bend to the loop and the body was often "anchored" with a loose coil. Although some individuals would occasionally crawl while holding this posture, none could be induced to strike.

The posturing and head triangulation defenses of *Dipsas oreas* resemble the defensive behaviors of some vipers (Greene, 1988) and thus are potentially a form of behavioral mimicry, and perhaps the banding pattern of *D. oreas* could resemble that of some vipers to certain predators. However, vipers are said by local residents not to occur at the Río Zaña Study Site, and none were recovered in my herpetofaunal sampling there (residents report "víboras" at lower elevations toward the coast; at least one species, *Bothrops roedingeri,* potentially occurs there, although this species is documented only farther south in the Peruvian coastal region; cf. Campbell and Lamar, 2004). In other parts of the range of *D. oreas,* a possibility exists that one or more viperid species is sympatric with *D. oreas,* judging from distribution maps in Campbell and Lamar (2004); however, such sympatry remains to be demonstrated. The only venomous species potentially occurring sympatrically with *D. oreas* at the Río Zaña Study Site is *Micrurus mertensi,* which is a coastal/foothill species (Campbell and Lamar, 2004) that is recorded in my collections from 1,300 to 1,400 m at the site, just short of the lowest recorded elevation for *D. oreas* (1,450 m). However, there is (to my perception) no particular resemblance between these two species.

Comparisons of Behavior with Other Species of Dipsas. Species of *Dipsas* occur in tropical dry forests and rain forests from central Mexico to the subtropical zone of southern Brazil, thus inhabiting an array of relatively aseasonal to highly seasonal environments. As indicated for the Río Zaña Study Site, seasonal activity correlated with the onset of rains or high ambient humidity has been reported in other species of *Dipsas* inhabiting seasonal environments. For example, Hartmann et al. (2002) found that adult *D. albifrons* were active only during the rainy season in the Atlantic forest of southeastern Brazil (juveniles seemed less seasonal in their activity). On the other hand, a related snake from the same region, *Sibynomorphus neuwiedi,* is more active during the cooler, drier season (Marques et al., 2001). Activity patterns of species of *Dipsas* from less seasonal rain forests in equatorial Amazonia do not show strong seasonality (e.g., Martins and Oliveira, 1998).

Cadle and Chuna (1995: footnote 5) commented on the seemingly paradoxical behavior of an arboreal snake such as *Dipsas oreas* retreating to the ground surface or subsurface during its inactive period, rather than seeking arboreal retreats. However, this behavior could be frequent in both montane and lowland members of the genus, as the following remarks indicate for several species.

Dipsas catesbyi: At La Selva Lodge (Río Napo, Ecuador) I found an adult *Dipsas catesbyi* (not collected) under dead leaves in deeply shaded forest at 1500 hr. At the same locality another individual encountered while active in low vegetation at night dropped to the ground after several minutes of observation and hid underneath the leaf litter. Comments associated with other specimens include "on ground

at night" (FMNH 165846; Colombia, Putumayo department) and "Under banana leaves on ground [presumably during the day] (FMNH 39640; Peru, Ayacucho department).

Dipsas indica: FMNH 165847 (Colombia, Putumayo department) was "on ground at daytime" (remarks in FMNH catalogue entry).

Dipsas latifasciata: LSUMZ 45499 (Peru, Pasco department) was "caught on ground of second growth at edge of humid forest in late afternoon." (remarks on field tag).

Dipsas peruana: USNM 299232–34, MUSM-JEC 6750 (Peru, Puno department). I collected these specimens inactive under rocks during the day. This locality was a somewhat dry rain shadow valley with xerophytic vegetation and few epiphytes to create arboreal retreats.

Observations of terrestrial activity for other species of *Dipsas* seem rarely to have been reported. Duellman (1978) reported terrestrial and arboreal activity for *D. catesbyi* in Ecuador. Orcés and Almendáriz (1987) reported, without stating whether the snakes were active or inactive, that neither *D. ellipsifera* nor *D. elegans* seemed to be arboreal snakes. At least one species, *D. pavonina* in central Amazonia, may be primarily terrestrial when foraging at night (Martins and Oliveira, 1998), although Duellman (1978: 240) reported arboreal activity for this species in western Amazonia. These examples suggest that diel movement between terrestrial retreats and arboreal microhabitats when nocturnally active may be common behaviors in some species of *Dipsas*, at least at some localities. Other species may even be terrestrial while active.[6] Conversely, many diurnal terrestrial snakes ascend vegetation to sleep at night, perhaps in response to carnivorous ants (Martins, 1993). At the Río Zaña Study Site, ants did not seem especially prevalent compared with my experience in lowland Amazonian rain forests; diurnal colubrids of genera known elsewhere to sleep in vegetation were never encountered sleeping in vegetation at the Río Zaña Study Site (e.g., *Chironius*, *Dendrophidion*, *Leptophis*, and *Mastigodryas*).

The factors that might affect where a snake seeks refuge during its inactive period are numerous, and individual, seasonal, geographic, and species-specific patterns of behavior are possible. Geographic trends may be related to the availability of arboreal retreats such as epiphytes—epiphytes are much more abundant in continually wet tropical rain forests than in more seasonal or subhumid forests (e.g., Myers, 1969). Bromeliads and other epiphytes are common at the Río Zaña Study Site, so the propensity for *Dipsas oreas* at that site to use terrestrial retreats when inactive is not because of the lack of appropriate arboreal ones. Bromeliads were routinely searched at the Río Zaña Study Site but yielded only frogs (*Eleutherodactylus* and *Gastrotheca*), and these only during the rainy season. The extended dry season at the Río Zaña Study Site results in low ambient moisture and humidity within the forest, and the surface of the soil, the leaf litter, and even many bromeliads become very dry. During the dry season, some streams at the Río Zaña Study Site temporarily cease flow, and the humidity is low enough that desiccation becomes a problem for the aerial egg clutches of centrolenid frogs laid toward the end of the rainy season (Cadle and McDiarmid, 1990). The factors combined probably explain the terrestrial seclusion behavior at this locality for *D. oreas*.

Although the observations reported here suggest that terrestrial seclusion for several species of *Dipsas* occurs with some frequency, other observations suggest that

[6] Movement between terrestrial retreats and arboreal active sites may be more widespread in tropical nocturnal, arboreal snakes than is currently recognized. In Madagascar, the colubrids *Geodipsas laphystia* and *G. zeny* are similar to species of *Dipsas*, in being nocturnally active in low vegetation (Cadle, 1996). However, both species are occasionally found hidden in moist leaf litter on the ground during the day (personal observations).

arboreal seclusion also occurs within *Dipsas.* Porto and Fernandes (1996) reported an inactive *D. neivai* found within a bromeliad on a tree branch close to the ground, and I collected an inactive *D. vermiculata* (MVZ 163259) from a bromeliad 2 m from the ground during the day. Parker (1926) reported that the type of *D. variegata trinitatis* was obtained from a bromeliad on a fallen tree. Charles W. Myers collected several inactive *D. temporalis* from bromeliads on the sides of trees 1.2–3 m aboveground during the day (Cadle and Myers, 2003: 36).

Eggs and Hatchlings. Cadle and Chuna (1995: 32–34) reported communal egg-laying in *Dipsas oreas* (21 total eggs), which in that instance was coincident with a large number of communally laid eggs of the gymnophthalmid lizard, *Macropholidus ruthveni.* The eggs, discovered 17 June 1987 at the lower edge of the humid forest (1,490 m) at the Río Zaña Study Site, were underground in a moist crevice within a road embankment. The eggs were 20–30 cm from the entrance to the crevice and 15 cm beneath the surface of the soil (the crevice ran somewhat parallel to the soil surface); dimensions of the *Dipsas* eggs were 28–30 × 20 mm. On the basis of their clustering within the crevice, the snake eggs probably represented three clutches of eight, seven, and six eggs. One egg was opened at the time from each of the two deepest clutches and contained advanced embryos of slightly different stages. Five of the eggs were transported in plastic bags containing moist paper towels back to an air-conditioned office, where they were kept in similar fashion on a table. These eggs hatched between 23 September and 1 October. Hatchlings (FMNH 232570–72, MUSM 16751–52) were 214–225 mm total length (172–176 mm SVL) and 2.8–3.2 g. A hatchling from this clutch is illustrated in Figure 17, and another was illustrated by Cadle and Myers (2003: fig. 11).

Two hatchlings or near-hatchlings of *Dipsas oreas* (MUSM 5530, 5532; total lengths 230–243 mm) were collected 13–15 January 1989 near the site where the above eggs were discovered. It seems likely that these hatchlings derived from eggs laid the previous dry season, as indicated by the eggs discovered in June and their slightly larger size than the above series of hatchlings.

Two other females of *Dipsas oreas* from Ecuador were gravid, and clutch sizes were estimated by palpation through the ventral body wall. ANSP 18117 (421 mm SVL) contained four eggs. BMNH 60.6.16.56 (566 mm SVL) contained about 8 eggs. No collection dates are available for these specimens.

Aggregation Behavior in *Dipsas oreas*

A peculiar aggregation of *Dipsas oreas* was discovered on 25 January 1989 at 1,800 m at the Río Zaña Study Site. At 10:15 a.m., a field assistant found a ball of four snakes on the surface of the leaf litter adjacent to a small log (10–15 cm diameter, 2.5 m long) in a somewhat disturbed patch of cloud forest; all of these snakes were intertwined in a tight ball. Another individual was on the leaf litter surface about 20 cm from the ball. After alerting me to the discovery we returned to the site and found another snake hidden under the leaf litter (15–20 cm deep) where the initial ball was found. At the opposite end of the log (2.5 m from the ball), another individual was hidden under the leaf litter. A search of the immediate area (surface and under logs, litter, etc.) turned up no more snakes. The night before finding the aggregation included a light drizzle for several hours; on the morning of the encounter, the leaf litter was wet and the day was overcast. Temperature at 11:00 a.m. was 15° C.

All snakes were quiescent and loosely or tightly coiled. The four snakes in the initial ball were completely and tightly intertwined, and consisted of an adult female and three adult males. The three individuals not associated directly with the ball were adult males. The female is ANSP

31784 and the males are ANSP 31779–81, 31783, 31785–86 (497–551 mm SVL; see Figs. 18, 19).

Aggregations of snakes occur for a variety of reasons, including hibernation (in temperate snakes), response to unfavorable temperature or humidity conditions, feeding, mating, and oviposition (e.g., Amr et al., 1997; Ford and Burghardt, 1993: 139–140; Gillingham, 1987: 197–198; Gregory et al., 1987: 370–373; Halpern, 1992; Noble and Clausen, 1936). The aggregation of *Dipsas oreas* just described seems unlikely to be due to unfavorable environmental conditions, hibernation, or feeding. The rainy season at the Río Zaña Study Sites commences in December or early January (as in 1989) and corresponds to the most active and environmentally favorable period for *D. oreas* and its gastropod prey. On the other hand, several observations suggest an association with reproductive behavior for the aggregation: all individuals are adults and all except one are males. This suggests that the aggregation may have been for mating, as does the morphology of the reproductive tracts described below. Unfortunately, the aggregation was disrupted before specific behaviors such as copulation or combat could be assessed. The fact that the aggregation was discovered during the day in a snake typically nocturnally active prompts questions that only additional serendipitous field observations could answer: Was this aggregation simply a continuation of courtship activity that had begun the previous night? Alternatively, do males locate females during the day?

Gregory et al. (1987: 370) defined aggregations as "any concentration of snakes in a relatively small area such that the density of snakes in the aggregation contrasts sharply with that in the surrounding area." Thus, aggregations need not involve continuous physical contact among individuals. In some snakes, males in mating aggregations are not necessarily continuously associated with the female, such as three of the males in the aggregation of *Dipsas oreas* just described. For example, Feio et al. (1999) observed six male *Chironius flavolineatus* courting a female, but only two were ever directly associated with the female, the other males being nearby on the ground or low bushes. Thus, even though three males were not directly associated with the tight cluster of *D. oreas*, it seems very unlikely that they were only coincidentally close by.

That the aggregation of *Dipsas oreas* described was associated with reproduction is also suggested by the morphology of the reproductive tracts of the female and males. The female (ANSP 31784) has small ovarian eggs (2–4 mm) in her left ovary. These are somewhat yellowish, perhaps indicating the initiation of yolk supply to the ova. Her left oviduct is extremely dilated (3.5–4 mm broad and thrown into many pleats), which is the condition observed in female snakes of many species prior to ovulation and fertilization (review in Fox, 1977). The middle portion and cranial end of the left oviduct, corresponding to the tube portion of the oviduct (Guillette et al., 1989), are particularly dilated and pleated. The right oviduct is less dilated than the left and not at all pleated. Except for a single ovum similar in size to those in the left oviduct, eggs in the right ovary are smaller and paler than those in the left ovary. These observations suggest that the left reproductive tract of the female was gearing up for reproduction. Moreover, the size of the ova in the left ovary correspond to follicle size classes II ("early growth") to III ("hydration and initial vitellogenesis") recognized for *D. catesbyi* by Zug et al. (1979: 2–3), which corroborates the other indications of reproductive competence of this female. The males in the aggregation have swollen and highly convoluted vasa deferentia, which are characteristic of male snakes during the breeding season.

Because so little is known of reproductive cycles and behavior of tropical snakes, it is worth exploring the details known for *Dipsas oreas* at the Río Zaña Study Site

and attempting to paint a scenario of what seems to occur. At the Río Zaña site, eggs of *D. oreas* with well developed embryos were discovered in mid-June in a well-secluded, relatively cool location deep within a crevice (details reported above). The advanced developmental stages of two embryos suggest that the eggs were laid some time prior to their discovery in mid-June. This observation, combined with the observed aggregation of several adult males and an adult female in late January, suggests that a mating period in late January may not be unreasonable. Moreover, the condition of the oviducts in the female and the vasa deferentia in the males suggest that these individuals were reproductively competent. The delay between the presumed mating period and egg laying would give ample time for fertilization and yolking of the ova.

In a related colubrid, *Sibynomorphus ventrimaculatus,* mating apparently takes place several months (perhaps as many as seven) before vitellogenesis commences and egg-laying occurs (Cechin and Oliveira, 2003). A similar sequence in *Dipsas oreas* would explain the small follicles in the female described above well before the inferred oviposition season. The strong seasonal activity pattern of *D. oreas* at the Río Zaña Study Site, as well as the few observations on eggs and hatchings, imply that reproduction is strongly seasonal in this species, at least in the southern part of its range. Other species of *Dipsas* that inhabit less seasonal environments of Amazonia or the Atlantic Forest of southeastern Brazil are apparently aseasonal in their reproductive patterns (Zug et al. [1979] for *D. catesbyi*; Porto and Fernandes [1996] for *D. neivai*), and some other members of the Dipsadini have extended periods of oviposition (e.g., two species of *Sibynomorphus*; Laporta-Ferreira et al., 1986).

Aggregation behavior is best known in north temperate species of natricine colubrids and viperids, although scattered observations of scolecophidians, elapids, and other groups of colubrids suggest that aggregation behavior is taxonomically widespread. Aggregations have previously been reported in three other species of Neotropical colubrids. An aggregation of *Rhadinaea calligaster* (Myers, 1974: 221) in a pile of decomposing thatch consisted of six females and a male. Females were apparently attracted to the site for oviposition because a communal nest was in the same pile of debris. The other cases involve aggregations for mating functions in snakes of the clade Colubrinae (*sensu* Cadle, 1984c, 1985): *Drymobius margaritiferus* (Campbell, 1998: 213) and *Chironius flavolineatus* (Feio et al., 1999). The observations reported here for *Dipsas oreas* constitute the first report of aggregation behavior in any species of Dipsadini (*Dipsas, Sibon, Tropidodipsas, Sibynomorphus*) and one of only three cases of mating aggregations in Neotropical colubrids. Because communal nests are now known in two distantly related members of the larger Neotropical clade Dipsadinae (*sensu* Cadle, 1984b; Zaher, 1999), *D. oreas* and *Rhadinaea calligaster,* aggregation behavior for oviposition may be widespread within this group if particular oviposition sites offer favorable conditions for egg development.

TAXONOMIC AND GEOGRAPHICAL NOTES ON *DIPSAS GRACILIS, D. LATIFASCIATUS,* AND *D. LATIFRONTALIS*

While studying the systematics of species in the *Dipsas oreas* complex and others in western Ecuador and Peru (e.g., Cadle and Myers, 2003) I had occasion to examine specimens of other species reported from the eastern and western versants of the Andes in this region. In a few cases, the specimens examined amplified distributional knowledge of species or raised questions concerning systematic and nomenclatural issues. I here comment on these points for three species. *Dipsas gracilis* has been well known from the western lowlands of Ecuador, but new in-

formation extends its range into Peru. *Dipsas latifasciatus* and *D. latifrontalis* have been reported from eastern Ecuador and/or Peru, but my examination of specimens disclosed some systematic and nomenclatural problems relative to the treatment of these species in the literature. Detailed locality data on specimens of these taxa I examined are given in the *Specimens Examined and Locality Records.* See *Note Added in Proof*, p. 136.

Dipsas gracilis

Dipsas gracilis (Boulenger, 1902) was not recorded south of Guayaquil, Ecuador (Peters, 1960a) until Tello (1998) reported it from a lowland (620 m) evergreen rain forest in extreme northwestern Peru on the basis of MUSM 17589 (Quebrada de los Naranjos, Tumbes department). I provisionally refer two additional specimens from northern Peru to *D. gracilis,* MUSM 2700–01 (Río Quiroz valley, Piura department). Although *D. gracilis* thus far has been reported in detail only from western Ecuador (Peters, 1960a; Peters and Orejas-Miranda, 1970), Perez-Santos and Moreno (1988, 1991) reported the species from Colombia without providing documentation. A specimen of *Dipsas* that I examined from northwestern Colombia near the Panama border (FMNH 74376) had been previously identified as *D. gracilis,* but I tentatively refer this specimen to *D. viguieri*; see comments in the following section (key to species) concerning some difficulties in distinguishing *D. gracilis* and *D. viguieri.* I here comment on characteristics of the Peruvian specimens of *D. gracilis,* whose scutellation and other characters are summarized in Table 4. Unfortunately, my examination of MUSM 17589 was brief, and basic data were not completed, although the specimen is well preserved. All three Peruvian specimens are males, so the most relevant comparison would be males of Ecuadorian *D. gracilis* (Table 4).

MUSM 17589 was obtained during a biological inventory of the lowland tropical forests of Tumbes department (Wust, 1998a). It is an adult male in excellent condition with well-everted hemipenes. The specimen has 22 broad black bands (encompassing 6–8 dorsal scale rows) that extend completely across the venter. Interspaces are whitish (3–4 dorsal rows in breadth) with brownish stippling concentrated in the central part of each interspace. The head is white with many irregular black markings on the top and sides.

Quebrada de los Naranjos, whence MUSM 17589 comes, is within a region of lowland humid tropical forest extending southward from Ecuador into far northwestern Peru (Chapman, 1926; Koepcke, 1961). This forest is the only truly lowland humid forest in western Peru and has never been extensive; remaining fragments are now a protected reserve (Wust, 1998a). Tello (1998:79) described the vegetation of Quebrada de los Naranjos as "an ephemeral thicket composed mostly of small plants of the Rubiaceae and ferns." Wust (1998b:22) stated that "In the hills of Quebrada de los Naranjos the forest is humid and evergreen, reaching more than 20 m in some parts, and with a more or less uniform canopy dominated by [*Ficus, Centrolobium, Vitex, Pouteria, Ocotea, Bombax,* and *Gallesia*]."

MUSM 2700–01 are assigned only provisionally to *Dipsas gracilis* because they are in poor condition (soft, poorly preserved, and with pattern elements obscure). The MUSM catalogues indicate that the specimens were collected 17 March 1966 (collector not listed) from the imprecise locality "Valle del Río Quiroz." Additional geographical indications in the catalogue (perhaps added later when the specimens were catalogued in Lima) include "Piura [department], Pv. [Provincia] Ayabaca." The Río Quiroz flows northwestward across extreme northern Piura department (western versant of the Andes) north of the Cordillera Guamani and eventually joins the Río Chira, which drains the southern part of Loja Province, Ecuador. Ayabaca Province is at the northern extremity of Piura department on the Ec-

TABLE 4. STANDARD CHARACTERS FOR PERUVIAN SPECIMENS REFERRED TO *DIPSAS GRACILIS* COMPARED WITH A SAMPLE FROM ECUADOR. HEAD SCALES ARE SCORED AS INDICATED IN TABLE 1. BILATERAL COUNTS ARE SEPARATED BY A SOLIDUS (LEFT/RIGHT). *N* = NUMBER OF SPECIMENS OR OBSERVATIONS; SVL = SNOUT TO VENT LENGTH.

	MUSM 2700 male	MUSM 2701 male	MUSM 17589 male	*Dipsas gracilis* Ecuador
Total length (SVL) (mm)				
Largest male	665 (471)	375 (275)	—	760 (524)
Largest female				727 (515)
Tail length/total length				
Male	0.29	0.27	—	0.30–0.33
				0.32 ± 0.01 (*N* = 6)
Female				0.29–0.31
				0.30 ± 0.01 (*N* = 3)
Maxillary teeth	18	—	—	17 (*N* = 1)
				19 (*N* = 1)
				24 (*N* = 2)
Dorsal scales	15-15-15	15-15-15	15-15-15	15-15-15
Ventrals (and preventrals)				
Male	187 (2 preventrals)	189 (1 preventral)	192 (1 preventral)	199–210 (1–5 preventrals)
				203.8 ± 3.97 (*N* = 6)
Female	—	—	—	194–199 (2–4 preventrals)
				196.0 ± 2.65 (*N* = 3)
Subcaudals				
Male	104	109	94	114–128
				120.7 ± 5.92 (*N* = 6)
Female	—	—	—	105–117
				109.0 ± 6.93 (*N* = 3)
Total segmental counts				
Male	291	298	286	313–333 (*N* = 6)
Female	—	—	—	298–316 (*N* = 3)
Anal scale	Single	Single	Single	Single
Loreal pattern	1	1	—	2 (*N* = 18)
Preoculars	1/1	1/1	—	0 (*N* = 18)
Postoculars	2/2	2/2	—	2 (*N* = 4)
				3 (*N* = 14)
Primary temporals	2/2	2/1	—	1 (*N* = 1)
				2 (*N* = 15)
				3 (*N* = 2)
Secondary temporals	3/3	2/2	—	2 (*N* = 11)
				3 (*N* = 7)

TABLE 4. CONTINUED.

	MUSM 2700 male	MUSM 2701 male	MUSM 17589 male	*Dipsas gracilis* Ecuador
Tertiary temporals	4/3	3/3	—	0 (N = 2) 3 (N = 14) 4 (N = 2)
Supralabials (touching eye)	11 (5–7)/11 (5–7)	10 (4–6)/11 (4–7)	—	8 (3–5) N = 1 9 (3–5) N = 3 9 (4–5) N = 4 9 (4–6) N = 2 10 (3–5) N = 1 10 (4–6) N = 7
Infralabials	13/13	13/13	—	10 (N = 1) 11 (N = 3) 12 (N = 8) 13 (N = 4)
Number of infralabials in contact behind mental	1 pair	2 pairs	1 pair	1 pair (N = 9)
Number of bands or blotches on body	24	21	22	13–19 (N = 9)

uadorian border. The general region is arid in lower reaches of the valley to the west and subhumid toward the east. Relictual patches of humid forest still existed in the 1990s at higher elevations in montane regions in the eastern part of the valley (personal observations; see above notes on habitats of *D. oreas* in northern Peru). *Dipsas gracilis* is otherwise known only from the lowlands (<1,000 m), whereas the only parts of the Río Quiroz valley presently having humid forest habitats are at higher elevations in the eastern part of the river system (>2,000 m).

The pattern elements visible in MUSM 2700–01 are similar to other specimens of *Dipsas gracilis*. The dorsal pattern consists of a series of dorsal blotches or bands, which, when viewed in lateral aspect, are oval on the anterior body and round posteriorly. The anterior bands nearly meet midventrally; posterior ones encroach onto the outer edges of ventrals. The top of the head is mainly dark blackish with light patches and flecks (more light patches are present in the smaller specimen, MUSM 2701). The vertebral scale row is greatly expanded (1.5–2× the width of the paravertebral rows).

The three Peruvian specimens referred to *Dipsas gracilis* conform generally to other males of *D. gracilis* I examined, but there are differences from Ecuadorian specimens as well (Table 4). The Peruvian specimens have lower ventral (187–192) and subcaudal (94–109) counts than males from Ecuador (ventrals 199–210, subcaudals 114–128). MUSM 2700–01 have shorter tails and a different loreal pattern from Ecuadorian specimens. In *D. gracilis* from Ecuador, all the dorsal bands are complete across the venter (anterior body) or encroach very broadly onto the ventral scutes, nearly meeting midventrally (posterior body). This is the case in MUSM 17589, but in MUSM 2700–01, the posterior bands end on the outer edges of the ventral scutes.

Although some scutellation characteristics of the three Peruvian specimens re-

ferred to *Dipsas gracilis* are outside the range of scale counts seen in Ecuadorian specimens of *D. gracilis*, they are likewise dissimilar to other species of *Dipsas* known from western South America in scutellation and/or color pattern. *Dipsas oreas* is also known from the "valley of the Río Quiroz" (Fig. 16, Fig. 23: locality 7), the locality for MUSM 2700–01. However, compared with characters of *D. oreas* males (Table 1 for total sample, Table 3 for Peruvian populations), MUSM 2700–01 have significantly greater numbers of ventrals, subcaudals, and supralabials. Moreover, the number of maxillary teeth of MUSM 2700 (18) is much greater than the number in a large sample of *D. oreas* (12–14; Table 1). Collection of additional material might permit a resolution of the systematic status of these Peruvian populations, particularly if new specimens of *D. gracilis* from the geographic gap between northern Peru and the vicinity of Guayaquil, Ecuador, can be obtained. Biogeographically, the presence of *Dipsas gracilis* in lowland humid forests of Tumbes department (MUSM 17589) was perhaps expected on the basis of other geographic and biological data from this region (e.g., Chapman, 1926; Koepcke, 1961), and MUSM 17589 is well documented in the context of a biological inventory (Wust, 1998a).

On the other hand, MUSM 2700–01 are more problematic because they are not accompanied by specific locality data or collector, and there may be reason to question their origin. Appropriate habitats do not apparently exist presently in the lowlands of the Río Quiroz valley, and *Dipsas gracilis* is otherwise known only from lowland localities. Moreover, *D. latifasciata* is recorded from inter-Andean valleys immediately east of the Río Quiroz (e.g., by MCZ 17404; see comments below). Most characteristics of the color pattern, scale counts, body proportions, loreal scale pattern, and maxillary tooth counts of MUSM 2700–01 are similar to those I recorded for *D. latifasciata* from the Amazonian versant of Peru and Ecuador (unpublished data). One characteristic of the patterns of MUSM 2700–01 is more typical of *D. latifasciata* than of *D. gracilis*: The posterior bands fail to encroach broadly onto the ventral scutes or to meet midventrally. If, in fact, MUSM 2700–01 were obtained from east of the continental divide or if *D. latifasciata* occurs on both versants of the Andes in this region, then the identity of these specimens should be reconsidered.

Dipsas latifasciatus and *D. latifrontalis* in Eastern Ecuador and Peru

Dipsas latifasciata (Boulenger, 1913) was described from the type locality "Upper Marañon, eastern Peru," and *D. latifrontalis* (Boulenger, 1905) has the type locality "Aricaqua" [Venezuela]; Peters (1960a: 110) identified the latter locality as the town of that name on the Amazonian slopes of the Andes in western Venezuela south of Mérida. These names and their applicability to populations in eastern Ecuador require further study. Without examining the holotype of either species, Peters (1960a) assigned specimens from eastern Ecuador to each. However, Peters' (1960a) characterizations reveal similar scutellation and few distinctions between them, such as whether some or none of the dorsal bands fail to meet midventrally, as stated in Peters' key (1960a: 33, couplet 35) or by the number of infralabial pairs in contact behind the mental. The last character is now known to be highly variable within species of *Dipsas*; for examples, see descriptions of the three species discussed in detail in this report or Cadle and Myers (2003) for *D. nicholsi* and *D. andiana*. There is broad overlap in the scutellation characters of these two taxa as construed by Peters (1960a). This in itself is not necessarily grounds for questioning their validity, but in combination with the other similarities noted by Peters and some inconsistencies in his own discussions (see below), it begs the question of how these nominal taxa are distinguished

and how the names should apply to Ecuadorian and Peruvian specimens.

Moreover, Peters (1960a) had little material of each species, particularly from near the type localities. He referred only three specimens from extreme southern Ecuador and northern Peru to *D. latifasciata.* More problematic was his referral of only one specimen from Venezuela to *D. latifrontalis* but, in addition, 44 others from eastern Ecuador. Thus, the distribution of "*Dipsas latifrontalis,*" as Peters (1960a: 99) conceived it, left a broad gap across eastern Colombia, from which no specimens referred to either of these species were reported. Peters himself seems to take great pains to justify his applications of these names to samples available to him based only on the type descriptions. Similarly, he justified his referral of the names *Leptognathus palmeri* Boulenger (1912) (type locality, "El Topo, Río Pastaza, Ecuador") and *L. praeornata* Werner (1909) (type locality, "Venezuela") to the synonymy of *Dipsas latifrontalis* by extended discussion of relatively few characters in the original descriptions (Peters, 1960a: 103, 109–110). The brevity of the original descriptions of all these taxa and the poor comprehension of intraspecific variability within *Dipsas* at the time of their descriptions mean that reference to the types is needed to resolve the systematics of these snakes.

These peculiarities and my interpretations of some material that both Peters and I examined lead me to question the proper name of specimens from eastern Ecuador and Peru. MCZ 17404, a specimen that Peters (1960a) assigned to *D. latifasciata,* has the pattern by which he characterized *D. latifrontalis* (all bands fail to meet midventrally). In fact, Peters (1960a: 103) stated that this specimen was "intermediate in some characters between what might be called typical *latifrontalis* and *latifasciata. . . .*" In three specimens that Peters assigned to *D. latifrontalis* from the same general area of Ecuador ("Llanganates Area" [probably southwestern Napo Province]), two (FMNH 23530–31) show the pattern characteristic ascribed to *D. latifrontalis,* whereas FMNH 23532, although it has a predominantly black venter, seems to have bands meeting midventrally, the pattern that Peters ascribed to *D. latifasciata.* Peters (1960a: 103) suggested the possibility that additional collections might "demonstrate that the relationship between [*latifrontalis* and *latifasciata*] is at best on the subspecific level."

Interpretive problems such as these suggest that a new look at snakes with the requisite characteristics from Venezuela, Ecuador, and Peru is warranted. As with many similar problems concerning species identities in *Dipsas,* adequate resolution will require renewed study of the types and other geographically proximate specimens. Consequently, Peters' assignment of specimens from eastern Ecuador to *D. latifrontalis* is unconvincing, as is his suggestion of a possible subspecific relationship between *D. latifrontalis* and *D. latifasciatus.* The specimens here referred to *D. latifasciata* (see *Specimens Examined and Locality Records*) are done so provisionally, pending further study of the Ecuadorian, Peruvian, and Venezuelan material (including types) referred to *D. latifasciata* and *D. latifrontalis.* Full resolution of the systematics of this group should also review the validity and proper synonymy of the names *Leptognathus palmeri* Boulenger (1912) and *L. praeornata* Werner (1909), which Peters considered synonyms of *D. latifrontalis* on the basis solely of the type descriptions.

KEY TO SPECIES OF *DIPSAS* IN WESTERN SOUTH AMERICA

I provide the following key to assist in identifying species and individual specimens of *Dipsas* in western South America. Six species of *Dipsas* are known from the western slopes of the Cordillera Occidental and adjacent Pacific lowlands of Ecuador and Perú: *D. andiana, D. elegans, D. ellipsifera, D. gracilis, D. oreas,* and *D.*

temporalis. All of these are known from Ecuador, but only *D. oreas* and *D. gracilis* have been reported from Peru. The key also includes three additional species known or expected in the Chocó region of Colombia: *Dipsas sanctijohannis, D. viguieri,* and (possibly) *D. nicholsi*; the last species, previously known only from central Panama (Cadle and Myers, 2003), has recently been recorded in eastern Panama near the Colombian border (Myers et al., unpublished data). Characters of *D. nicholsi* and *D. andiana* in the key are based on diagnoses given in Cadle and Myers (2003) and another female of *D. nicholsi* reported by Myers et al. (ms.). The differential characteristics of *D. sanctijohannis* in the key are based on data from Peters (1960a) and on data kindly provided by Charles W. Myers from specimens he examined. Characters of all other species are based on discussions in this paper (*D. elegans, D. ellipsifera, D. gracilis, D. oreas*) or unpublished data (*D. temporalis*) in conjunction with some data from Peters (1960a).

Without additional study, I am unable to adequately differentiate *Dipsas viguieri* (eastern Panama and northern Chocó, Colombia) and *D. gracilis* (western Ecuador and extreme northern Peru). Geography currently seems to be the only reliable means of assigning names to specimens of these species. The characters that Peters (1960a) used to distinguish *D. viguieri* and *D. gracilis* (e.g., preocular presence/absence, number of postoculars) are known to be highly variable intraspecifically within *Dipsas*. Peters (1960a: 52) considered the two perhaps only "subspecifically distinct" and otherwise noted (Peters, 1960a: 48) that "The characters separating [*Dipsas gracilis*] and *D. viguieri* are comparatively weak ones. . . ." Thus, specimens of *D. viguieri* will key out to *D. gracilis* with this key. The differential characters (if any) of these two species and the disjunction (or lack thereof) between their ranges in western Colombia require further research. Nonetheless, if these two taxa are closely related or conspecific, then they would add a third example within *Dipsas* of a biogeographic connection between northwestern (Chocoan) South America and eastern Panama. The other examples are *D. andiana–D. nicholsi* (Cadle and Myers, 2003) and *D. temporalis*, which has scattered records from northwestern Ecuador into eastern Panama.

In addition to illustrations provided herein, illustrations and discussions of some of the relevant taxa are found in Peters (1960a; *D. gracilis*, pl. Ib, c and *D. ellipsifera*, pl. IVa), Kofron (1982; *D. elegans, D. ellipsifera,* and *D. oreas*), and Cadle and Myers (2003; *D. andiana, D. nicholsi,* and *D. oreas*). The key is dichotomous except for the last numbered section, a triplet.

1. Dorsal bands very broad anteriorly and posteriorly, covering 8 or more dorsal scale rows in longitudinal dimension; bands continuous, or nearly so, across the venter at least anteriorly. Subcaudals >90, often >100 (up to 132). Tail ≥29% of total length. Either no infralabials in contact behind the mental scale, or one pair in contact 2
– Dorsal bands narrower, covering 10 or fewer dorsal scale rows in longitudinal dimension (usually <7); anterior bands usually much broader than posterior bands, and all bands end on outer edges of ventrals or on lowermost dorsal rows. Subcaudal counts variable, but usually <100 (except male *D. andiana*, up to 106). Tail ≤28% of total length. At least one pair of infralabials in contact behind the mental scale 3
2. No infralabials in contact behind the mental scale. Anterior pair of chin shields very small (in contact with mental), followed by a pair of much larger chin shields. ..... *Dipsas temporalis* (Werner) (eastern Panama, western [Chocoan] Colombia, and western Ecuador; primarily in low uplands in Panama, 800–1,000 m; apparently also in the lowlands in Colombia and Ecuador)
– One pair of infralabials in contact behind the mental scale. Anterior pair of chin shields about the same size as, or only slightly smaller than, the second pair. ..... *Dipsas gracilis* (Boulenger) (lowlands [150–620 m] of western Ecuador from just north of the equator to extreme northwestern Peru [Tumbes and, less cer-

tainly, Piura departments; see discussion herein]) [*D. viguieri* will also key here]

3. A distinct V- or U-shaped mark with well-defined, regular borders on top of the head (apex anteriorly at frontal/prefrontal border); head otherwise pale brown or grayish brown and relatively unmarked. Ventrals ≥185 in males and females. Subcaudals >90 in males, ≥82 in females. 4
– No distinct stereotypic inverted V- or U-shaped mark on the top of the head.[7] Head usually with many dark markings, including darkened suture lines; entire head may be dark. Ventrals <190 in males and females. Subcaudal counts variable, but often much less than 80 5
4. Ventrals 185–196 in males, 185–191 in females. Subcaudals 91–106 in males, 82–83 in females. Branches of the V-shaped mark on top of head generally not connected to the first pair of neck blotches. Dorsal blotches at midbody taller than wide. ..... *Dipsas andiana* (Boulenger) (lowlands and lower montane slopes of western Ecuador from approximately the equator to latitude 2°S; 5–1,140 m)
– Ventrals 198–208 in males, 200–206 in two females. Subcaudals 92–98 in males, 87–95 in females. Branches of the V-shaped mark on top of head connected to the first pair of neck blotches. Dorsal blotches at midbody wider than tall. .... *Dipsas nicholsi* (Dunn) (lowlands <200 m in the Río Chagres basin of central Panama; Darién highlands, 875 m, of extreme eastern Panama; Myers et al., ms.)
5. Ventrals 153–164 in males, 157–158 in two females. Subcaudals 72–78 in males, 62–63 in two females ... *Dipsas ellipsifera* (Boulenger) (known only from the valley of the Río Mira in extreme northwestern Ecuador, 570–2,600 m)
– Ventrals >165 in males and females. Subcaudals >80 in males, >70 in females 6
6. Subcaudals 82–91 in males, 70–83 in females. Top of head usually with a pair of large elongate irregular blotches centered on the parietal region. Head otherwise with many dark spots and flecks and darkened suture lines. Thirty or fewer bands on the body, with anterior bands covering more than 5 dorsal rows in longitudinal dimension. Each band in adults usually with a somewhat pale central portion, but bands in most specimens without distinct borders enclosing a highly contrasting pale central area. Anterior bands end on outer edges of ventrals. Venter dirty whitish to grayish, usually with many small dark irregular spots and streaks ..... *Dipsas oreas* (Cope) (western Ecuador and northwestern Peru, approximately latitude 2°S to nearly 7°S; primarily Andean foothills and slopes, 1,400–2,600 m; lowlands in the vicinity of Guayaquil, Ecuador)
– Subcaudals 94–105 in males, 68–88 in females. Top of head with many dark brown irregular marks on a pale brown ground color, but generally not forming paired irregular blotches and occasionally nearly solid dark brown. Twenty-five to 46 bands on body. Each band in adults comprising a pair of bold blackish vertical edges enclosing a contrasting pale brown central portion. Anterior bands cover no more than 5 dorsal scale rows and end on outer edges of ventrals. Venter grayish with many small dark flecks and squarish markings, which sometimes form longitudinal arrays ..... *Dipsas elegans* (Boulenger) (western Ecuador from just north of the equator to approximately latitude 1°10′S, 500–2,650 m)
– Subcaudals 86–94 in males, 70–83 in females. Top of head in adults relatively uniform medium brown (dark-spotted in juveniles). Twenty-one to 28 bands on body; anterior bands complete or nearly complete across venter; each band solid, without pale central portion. Venter brown without numerous dark flecks and spots ..... *Dipsas sanctijohannis* (Boulenger) (Colombia: western slopes of the Cordillera Occidental in Chocó and the inter-Andean valley of the Río Cauca)

[7] The elongate blotches on the parietal region in *Dipsas oreas* occasionally fuse to form an irregular V-shaped mark that is very different from the marking in *D. andiana*. See Cadle and Myers (2003: 24, fig. 11).

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SPECIMENS EXAMINED AND LOCALITY RECORDS

A few literature records are included herein when there is reason to be assured of the identity of the specimens, which is rarely the case with South American species of *Dipsas.* Some of these records are discussed in the above species accounts (see sections on *Distribution*). In addition to specimens of the three species of the *oreas* group, this list also includes material of *D. gracilis, D. latifasciata,* and *D. temporalis* examined during the course of this study. This should aid future workers on this genus because many of the identifications in the literature are questionable and much material has accumulated since the group was last reviewed (Peters, 1960a). Discussion of some apparent problems concerning the systematics of *D. gracilis* and *D. latifasciata* is given in the text. Other material relevant to the identity of species in western Ecuador was listed in Cadle and Myers (2003) (*D. andiana, D. nicholsi,* and *D. variegata*).

Institutional abbreviations for museums are as follows.

AMNH	American Museum of Natural History, New York
ANSP	Academy of Natural Sciences of Philadelphia

BMNH	The Natural History Museum, London
FMNH	Field Museum of Natural History, Chicago
KU	Museum of Natural History, University of Kansas, Lawrence
LSUMNS	Museum of Natural Science, Louisiana State University, Baton Rouge
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
MUSM[8]	Museo de Historia Natural de San Marcos, Lima, Peru
MNHN	Muséum National d'Histoire Naturelle, Paris
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley
UMMZ	Museum of Zoology, University of Michigan, Ann Arbor

Dipsas elegans

ECUADOR: "Tehuantepec" [Oaxaca, Mexico], in error (see text), BMNH 1946.1.21.77 (holotype). "Western Ecuador," BMNH 60.6.16.73. **[PROV. CHIMBORAZO]:** Pallatanga [1,500 m; 01°59′S, 78°57′W], BMNH 80.12.5.267. **PROV. COTOPAXI:** Corazón [900–1,200 m; 01°08′S, 79°04′W], USNM 210938–39.[9] **PROV. PICHINCHA:** Way to Mindo [0°2′S, 78°48′W], USNM 210934, 210961 (see footnote 9). 2.9 km SW Tandayapa on Mindo Road, 1,820 m [0°1′S, 78°46′W], USNM 285957. Nanegal Grande [about 1,400 m; 0°7′N, 78°40′W], USNM 210936. Below Pacto, [1,200 m; approximately 0°8′N, 78°45′W], USNM 210937. Río Saloya, 4,000 feet [1,220 m; 0°1′N, 78°57′W], BMNH 1940.2.20.32. Santo Domingo de los Colorados [500 m; 0°15′S, 79°9′W], USNM 210935. Perucho [1,830 m; 0°6′N, 78°25′W] (Orcés and Almendáriz, 1987]. El Quinche, 2,640 m [0°6′S, 78°17′W] (Orcés and Almendáriz, 1987). Cumbayá, 2,354 m [0°12′S, 78°26′W] (Orcés and Almendáriz, 1987). Chiriboga, 1,800 m [0°15′S, 78°44′W] (Orcés and Almendáriz, 1987). Tumbaco [2,400 m; 0°13′S, 78°24′W] (Orcés and Almendáriz, 1987). **PROV. IMBABURA:** Near Peñaherrera-Intag, 1,500 m [0°21′N, 78°31′W], UMMZ 92073.

Dipsas ellipsifera

ECUADOR: [PROV. IMBABURA]: Ibarra [=Ybarra; 2,211 m; 0°21′N, 78°7′W], BMNH 1946.1.21.26 (formerly 98.4.28.87) (syntype), BMNH 1946.1.21.27 (formerly 98.4.28.89) (syntype), BMNH 1946.1.21.28 (formerly 98.4.28.88) (syntype), BMNH 1946.1.21.29 (formerly 98.4.28.90) (syntype), MCZ 8431. Lita, 572 m[10] [0°52′N, 78°28′W] (Orcés and Almendáriz, 1987). Chachimbiro, 2,600 m [0°27′N, 78°13′W] (Orcés and Almendáriz, 1987). Pimampiro, 2,000 m [0°30′N, 77°56′W], UMMZ 83697–700.

Dipsas gracilis

ECUADOR: PROV. ESMERALDAS [?PROV. PICHINCHA]:[11] Hacienda Equinox, 30 km NNW Santo Domingo de los Colorados, 1,000 ft. [305 m; approximately 0°5′N, 79°8′W], USNM 210945. **PROV. GUAYAS:** near Guayaquil [approximately 2°10′S, 79°50′W], USNM 210947. **PROV. PICHINCHA:** 47 km S. Centro Científico Río Palenque, 150–220 m [approximately 0°50′S, 79°30′W], USNM 286478–80. Centinela, 14.1 km SE Patricia Pilar by road, 570–600 m [0°37′S, 79°18′W], MCZ 156894. Santo Domingo de los Colorados [0°15′S, 79°9′W], USNM 286477. Centro Científico Río Palenque [200 m; 0°33′S, 79°22′W], MCZ 147183. Estación Biológica Río Palenque, 56 km N Quevedo, 220 m [0°33′S, 79°22′W], KU 152604.

PERU: DEPTO. TUMBES: Quebrada Los Naranjos, 3°50′S, 80°14′W, 620 m, MUSM 17589.

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[8] MUSM-JEC refers to Cadle field numbers for which the MUSM catalogue numbers are not yet available.

[9] USNM specimens from "Corazón" (USNM 210938–39) and "Way to Mindo" (USNM 210934, 210961) are probably equivalent in whole or in part to EPN 717–718 ("El Corazón") and EPN 719 ("camino a Mindo") cited by Peters (1960a: 92) as "*Dipsas ellipsifera.*" According to USNM records, these specimens were obtained by Peters from Gustavo Orcés-V. and recorded originally as "GOV 717–719" (Steve Gotte, personal communication, October 2004). Orcés-V. was, at the time, curator at the EPN.

[10] I confirmed the elevation of Lita given by Orcés and Almendáriz (1989) on two maps ("República del Ecuador" 1:1,000,000 published by the Instituto Geográfico Militar [Quito], 1991; and "Ecuador" 1:1,000,000 published by ITMB Publishing, Vancouver, 1994–1996). Paynter (1993) gave 900 m as the elevation.

[11] My maps place this locality, as given by distance from Santo Domingo de los Colorados, in Pichincha Province. The specimen was obtained by James A. Peters, who used "Esmeraldas Province" in his field notes and as registered in the USNM catalogues (S. Gotte, personal communication, September 2004). Data on a paper label within the jar differ slightly from the catalogue data: 32 km NNW Santo Domingo de los Colorados and "James Brown Farm," rather than "Hacienda Equinox."

Dipsas gracilis(?)

PERU: DEPTO. PIURA: Provincia Ayabaca, Valle del Río Quiroz [approximately 4°45′S, 79°50′W], MUSM 2700–01.

Dipsas latifasciata

ECUADOR: PROV. NAPO: Coca [0°28′S, 76°58′W], MCZ 166589–90. El Reventador [approximately 0°40′S, 77°40′W; locality assumed to refer to lower eastern slopes of Volcán El Reventador, a high peak in the eastern cordillera], MCZ 164510–11. 21 km SSW Reventador, 1,700 m [approximately 0°7′S, 77°38′W; Lynch and Duellman, 1980: 85], KU 164212. Lumbaqui [0°3′N, 77°20′W], MCZ 164674–75.

PERU: [DEPTO. CAJAMARCA]: Tabaconas [1,892 m; 5°19′S, 79°18′W], MCZ 17404. **[DEPTO. SAN MARTÍN/LORETO]:** Cumbre Ushpayacu-Mishquiyacu, 3,200 feet [975 m; 6°57′S, 76°3′W],[12] AMNH 52444. **DEPTO. PASCO:** Playa Pampa, about 8 km NW Cushi on trail to Chaglla, 2,100 m [9°57′S, 75°42′W[13]], LSUMZ 45499.

Dipsas oreas

ECUADOR: "The elevated Valley of Quito" (probably southern Ecuador, as discussed in the text), ANSP 10115 (holotype). "Western Ecuador," BMNH 60.6.16.56, 60.6.16.63. **PROV. CHIMBORAZO:** Alausí, 2,390 m [2°12′S, 78°50′W] (Despax, 1911: 36, as "*Leptognathus mikani*"). **PROV. CHIMBORAZO/CAÑAR:**[14] Huigra to Río Chiguancay [2°13′S, 79°3′W], ANSP 18117, 18120, 18123. [Río] Chanchan Valley [approximately 2°17′S, 79°24′W], MCZ 17083, UMMZ 56491. **PROV. GUAYAS:** Guayaquil [2°10′S, 79°50′W], USNM 60006, 62797–802. **PROV. LOJA:** Catamayo Valley, 9,780 feet [2,982 m; approximately 4°5′S, 79°35′W], USNM 98923. "Loja, Nouvelle-Grenade" [inferred to be the city of Loja, 2,200 m; 4°S, 79°13′W], MNHN 6285 (holotype of *Leptognathus andrei* Sauvage, 1884; see Kofron, 1982: 48–50]. 13 km E Velacruz (20 km NE Catacocha), 2,250 m [3°58′S, 79°33′W], KU 142803.

PERU: DEPTO. PIURA: Immediate vicinity of Ayabaca, approximately 2,600 m [4°38′S, 79°43′W], MUSM-JEC 10347. Toronche (town at base of Cerro Aypate), approximately 16 km (airline) SE Ayabaca, 1,950 m [4°35′S, 79°32′W], MUSM 16750. 2 km W Porculla [Pass] [5°51′S, 79°31′W], MVZ 119330. About 15 km (by road) E Canchaque on road to Huancabamba [about 5°24′S, 79°36′W], LSUMNS 27373.[15] **DEPTO. CAJAMARCA:** Río Zaña Study Site, 1,450–1,800 m [6°51′S, 79°6′W; see *Materials and Methods* for interpretation of this locality], ANSP 31777–81, 31783–86; FMNH 232570–72, 232575; MUSM 3361, 3452, 5530, 5532–33, 16751–52.

Dipsas temporalis

COLOMBIA: DEPTO CHOCÓ: Agua Clara, Río Tamaná [approximately 4°53′N, 76°45′W], USNM 267244. **PANAMA: [PROV. PANAMÁ]:** Pequeni-Chagres ridge, head of Rio Limpio and Quebrada Las Tres Honeras (Panama snake census) [9°18′N, 79°27′W], MCZ 50214. South slope of Cerro La Campana, 850 m [8°43′N, 79°54′W], KU 110293. **PROV. DARIÉN:** Ridge between Río Jaque and Río Imamadó, 800–890 m [7°35′N, 77°57′W; see Cadle and Myers, 2003: fig. 16], KU 110294–96. North ridge of Cerro Cituro, Serrania de Pirré, 900–1,000 m [approximately 8°5′N, 77°46′W], KU 110298–110301.

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[12] The specimen is part of the Harvey Bassler collections from eastern Peru (see Myers, 2000: 139–141). The locality is along a ridge separating the headwaters of the Río Mishquiyacu (Río Huallaga drainage) and the Río Uchpiyacu (Río Ucayali drainage) and forming the border between San Martín and Loreto departments. The Mishquiyacu flows westward into the Río Huallaga near the town of Pilluana. The Uchpiyacu flows eastward into the Río Cushabatay, a tributary of the Río Ucayali.

[13] Coordinates from Dr. Thomas S. Schulenberg, who collected the specimen.

[14] Lower reaches of the Río Chanchan form the border between Chimborazo and Cañar provinces. Huigra itself is in Chimborazo province.

[15] Another specimen from near Canchaque collected in the early 1990s is in the Museo de Historia Natural de la Universidad Privada Antenor Orrego (Trujillo, Peru). It is referable to *Dipsas oreas* on the basis of color pattern (I examined the specimen briefly in 1994 but did not complete details such as scale counts).

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NOTE ADDED IN PROOF: Paulo Passos kindly called my attention to Fernandes et al. (2002), in which *Dipsas latifasciatus* is synonymized with *D. polylepis*. These authors could not resolve the status of *D. polylepis* vis-à-vis *D. latifrontalis*.

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The Orb-Weaver Genus *Mangora* of Mexico, Central America, and The West Indies (Araneae: Araneidae)

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THE ORB-WEAVER GENUS *MANGORA* OF MEXICO, CENTRAL AMERICA, AND THE WEST INDIES (ARANEAE: ARANEIDAE)

HERBERT W. LEVI[1]

ABSTRACT. Thirty-two species of *Mangora* are found in the region under consideration. Three temperate species extend their ranges into northern Mexico, three Mexican species extend into the Southwest, and four species extend into South America. Only one species, *M. melanocephala* from Central America and South America, is both widespread and common. One species is found in the West Indies, including Trinidad. Of the 32 species, 15 are new. Six new synonyms are found. A few synapomorphies place *Mangora* close to *Araneus*.

INTRODUCTION

At present, Mexican and Central American *Mangora* can be determined only with the 1894–1904 publications of O. P.- and F. O. P.-Cambridge in the Biologia Centrali-Americana (on Guatemalan spiders mostly, but including some from Tabasco, Mexico), and Chickering's two papers (1954, 1963) on Panamanian *Mangora*. They deal with only a small part of the region. *Mangora* of most of the region remain unknown and undetermined collections have accumulated in museums. The inability to recognize species of the region has limited needed work on ecology, behavior, and physiology of the genus. *Mangora pia* was used by Craig (1987a,b, 1988, 1989) for her observations on behavior and structure of silk.

Distinctiveness of most South American *Mangora* species make it advisable to publish on the species of Mexico, Central America, and the West Indies (excluding Trinidad) and to deal with the many species of Trinidad and South America separately. The astonishing abundance of tropical South American *Mangora* species, mostly undescribed, may make this the most species-rich genus of araneids in the Americas.

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METHODS

Preserved *Mangora* specimens are more fragile than other araneid specimens. It is nearly impossible to avoid breaking leg macrosetae when handling. For examination, specimens were placed on a substrate such as black paraffin with suitable depressions, black silicon carbide crystals (80 grit), or black Velcro tape glued to a dish. The black background minimizes reflections.

Description. Alcoholic specimens were used to describe coloration even though many have some bright coloration that washes out. No color slides were available to show the color when alive.

Eyes. Eyes in araneids are difficult to measure because the curved cornea extends beyond the eye as seen from above. Thus, eyes seen from the side appear larger than when viewed from above. There also is individual variation in eye placement. Eye measurements are rough estimates.

The line of posterior eyes was checked against an imagined line behind the eyes when viewing the eyes dorsally. An imaginary line outside of the eyes, when seen from above, defined the median eye trapezoid. Despite the difficulty in measuring, numerical sizes and distances are given. Approximations are easier to describe in numbers than in words.

Measuring. Total length was measured without stretching the animal, whose elongate abdomen hangs at an angle with the prosoma (Levi, 1975, fig. 59; 2002, fig. 2). Length of body parts and leg articles are accurate only to 0.1 mm because legs were not amputated and leveled for measurements.

Figures. Figures of holotypes of species north of Mexico were made in 1970 (Levi, 1975). Here, the tips of palpi are additionally illustrated, perhaps making them easier to determine without amputating the structure. The apical view also helps to distinguish relationship of the complicated sclerites without expanding the palpus.

The ventral view of epigyna is often illustrated from slightly anterior. Lifting the epigynum with a needle or folding it back exposed the posterior view. The epigyna were cleared with Hoyer's medium. Individual specimens of *Mangora* less than 2.5 mm in total length were submerged in the clearing medium. In larger specimens, the epigynum was removed and cleared for examination and later stored in a small vial with the rest of the specimen.

The directions for locating structures in the illustrations (h) refer to the numbers in the face of a clock.

Maps. Maps were made with a computer. Collecting sites were located with various automobile maps and the gazetteers of the United States Board on Geographic Names (1956, 1965), Office of Geography, Department of the Interior. A gazetteer of the localities of the Cambridges' types is given by Selander and Vaurie (1962). Collectors of specimens often published maps of their collecting sites (e.g., Goodnight and Goodnight, 1953; Petrunkevitch, 1909; Vaurie and Vaurie, 1949).

Specimens Used. Specimens used came from the following collections and individuals:

AD	A. Dean, Texas A&M University, College Station, Texas, United States
AMNH	American Museum of Natural History, New York United States; W. J. Gertsch, J. A. L. Cooke, N. Platnick
BMNH	Natural History Museum, London, United Kingdom; P. Hillyard, J. Beccaloni
CAS	California Academy of Sciences, San Francisco, California, United States; C. Griswold, D. Ubick
CNC	Canadian National Collections, Ottawa, Ontario, Canada; C. Dondale
CUC	Cornell University Collection kept in the AMNH
ECOSUR	ECOSUR Collection, Chetumal, Quintana Roo, Mexico; G. Alayón
FSCA	Florida State Collection of Arthropods, Gainesville, Florida, United States; G. B. Edwards
HEF	The late Harriet Exline Frizzell, W. Peck, kept in CAS
JM	J. M. Maes, León, Nicaragua
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts, United States; G. Giribet
MIUP	Museo de Invertebrados, Universidad de Panamá, Panamá Panamá; D. Quintero A.
MNHN	Museum National d'Histoire Naturelle, Paris, France; M. Hubert, C. Rollard
NMB	Naturhistorisches Museum, Basel, Switzerland; E. Sutter, A. Hänggi
PAN	Polish Academy of Science, Warsaw, Poland; J. Proszynski, A. Slojewska
REL	Robin E. Leech, Edmonton, Alberta, Canada
SMF	Senckenberg Museum, Frankfurt am Main, Germany; M. Grasshoff
USNM	National Museum of Natural History, Washington, D.C., United States; J. Coddington

TAXONOMIC SECTION

Mangora O. P.-Cambridge

Mangora O. P.-Cambridge, 1889: 13. Type species: *Mangora picta* O. P.-Cambridge from Guatemala, designated by Simon, 1895: 793. Levi, 1975: 116.

Diagnosis. Mangora differs from all other araneid genera by the presence of feathered trichobothria on the tibia of the third leg (unfortunately often broken off in poorly handled specimens) (Levi, 1975, fig. 59; 2002, fig. 2). Easier to observe is the unique shape of the carapace: it is bald and narrow in the eye region, usually only one-half or less of the total width of the carapace, and the thoracic region of the carapace is high, equal to or greater than the width of the carapace in the eye region. The high thoracic region slopes evenly toward the eye region (Levi, 1975, fig. 59; 2002, fig. 2). Unlike most araneids, the abdomen is always oval, longer than wide (Figs. 3, 4, 10). The thin legs have long, strong macrosetae, which stand up, not appressed against the appendage (Levi, 1975, fig. 59; 2002, fig. 2). First legs are subequal in length with the fourth. Discrete black frames of the posterior median eyes (Levi 1975, fig. 58), and the posterior eye row being procurved in some species, further distinguish *Mangora*.

Description of Female. The venter of the female abdomen is often unmarked. The posterior eye row can be straight, recurved, or procurved. The anterior median or posterior median eyes are the largest, the laterals smallest, the posterior laterals always slightly smaller than the anterior. The clypeus height is usually equal to the diameter of the anterior median eyes. The first and fourth legs are subequal in length; the fourth is often thicker than the first. Individual specimens of a species vary in darkness of their coloration.

Description of Male. The male has similar but lighter coloration than the female. The eyes are slightly closer to each other than in the female. The endite tubercle is minute, often hard to see or just a tiny swelling. The hook on the first coxa is always present; it may be very small and shifted posteriorly.

The male genitalia are surprisingly complex. There is always a radix (R), a median apophysis (M), and a soft conductor (C) holding the tip of the embolus (E) (Figs. 89, 90). The embolus is of variable shape, rarely filiform. The terminal apophysis (A) is complex and of enormous size, with soft and hard lobes, difficult to figure out unless expanded (Figs. 89, 90). The palpal patella has always one strong seta.

Sizes. Many of the tropical *Mangora* are small, females 2.0 to about 7.0 mm total length, males 1.5–4.5 mm. The largest here is *Mangora pia,* found in Panama and observed by Lubin (1978) and used for experiments by Craig (1987–1989).

Relationship. Relationship with *Araneus* is suggested by the frequent presence of a scape with a distal pocket in the epigynum of the female (Figs. 62, 97, 110), and in the palpus of the male, the conductor close to the rim, median apophysis with spines (Figs. 89, 90), without a paramedian apophysis, and the presence of a large terminal apophysis. This agrees with the cladogram of Scharff and Coddington (1997).

Distribution. Thirty-two species are found in Mexico and Central America, 15 of them new. Of these 32, 3 temperate species extend their range into northern Mexico (*M. gibberosa, M. placida,* and *M. spiculata*) and 3 Mexican species extend into the Southwest (*M. calcarifera, M. fascialata,* and *M. passiva*). Four species also are found in South America (*M. amchickeringi, M. falconae, M. melanocephala,* and *M. pia*; Maps 1, 2). *Mangora melanocephala,* the most common *Mangora,* is also the most widespread, from the Isthmus of Tehuantepec to Peru and Brazil (Map 1E). Only one species, *M. fascialata,* is found in the West Indies excluding Trinidad (Map 2A).

Names. An attempt was made to not use specific names used before in the family.

Distinguishing Characters of Species. For separating *Mangora* species, examination of the color pattern is useful, and it is essential to examine not only the ventral view of the epigynum, but also the posterior view (Figs. 2, 9, 15), by lifting the epigynum with a needle or folding it over. Internal genitalia do not provide good characters to separate species.

Males generally are similar to females in color pattern. Their palpi are so complex that only a slight twist of the palpus provides a different image (Figs. 5–7).

Unrecognizable Species. I start systematic revisions by checking catalogs (Platnick, 2004; Roewer, 1942). According to these catalogs, *Zilla decolorata* Keyserling, 1893, is described from Brazil. I borrowed the holotype from BMNH and found it to be a male collected in Bahia, Brazil, and the type is marked *Zilla decolorata* (C. L. Koch). Koch described a *Zilla decora,* listed in Volume 3 of Bonnet (1961) as *decolorata,* but it comes from Germany and is a synonym of *Mangora acalypha* (Walckenaer, 1802). Although *Zilla decolorata* Keyserling had been placed in *Araneus* and *Zygiella,* the male examined was a *Mangora.*

When working on the Brazilian *Mangora* and checking original literature, I found to my surprise that *Zilla decolorata* was described from a female from Guatemala. Now that I have seen most Central American *Mangora,* I do not recognize it. It is relatively large, total length 5.9 mm, but in Central America, only *Mangora* with a pair of posterior rectangular black spots are this large. Most *Mangora* are smaller. It might be *Chrysometa lancetilla* Levi (Tetragnathidae) but *Chrysometa* has shorter fourth legs than those Keyserling measured for *Zilla decolorata.*

Bonnet (1957) cites Petrunkevitch (1911) as writing that *Z. decolorata* also appears in Brazil, but Petrunkevitch (1911) indicated that it is found in Guatemala. (A line below cites a spider from Brazil.) I consider the name unrecognizable.

KEY TO FEMALE *MANGORA*

Female of one species, *M. sufflava,* is not known

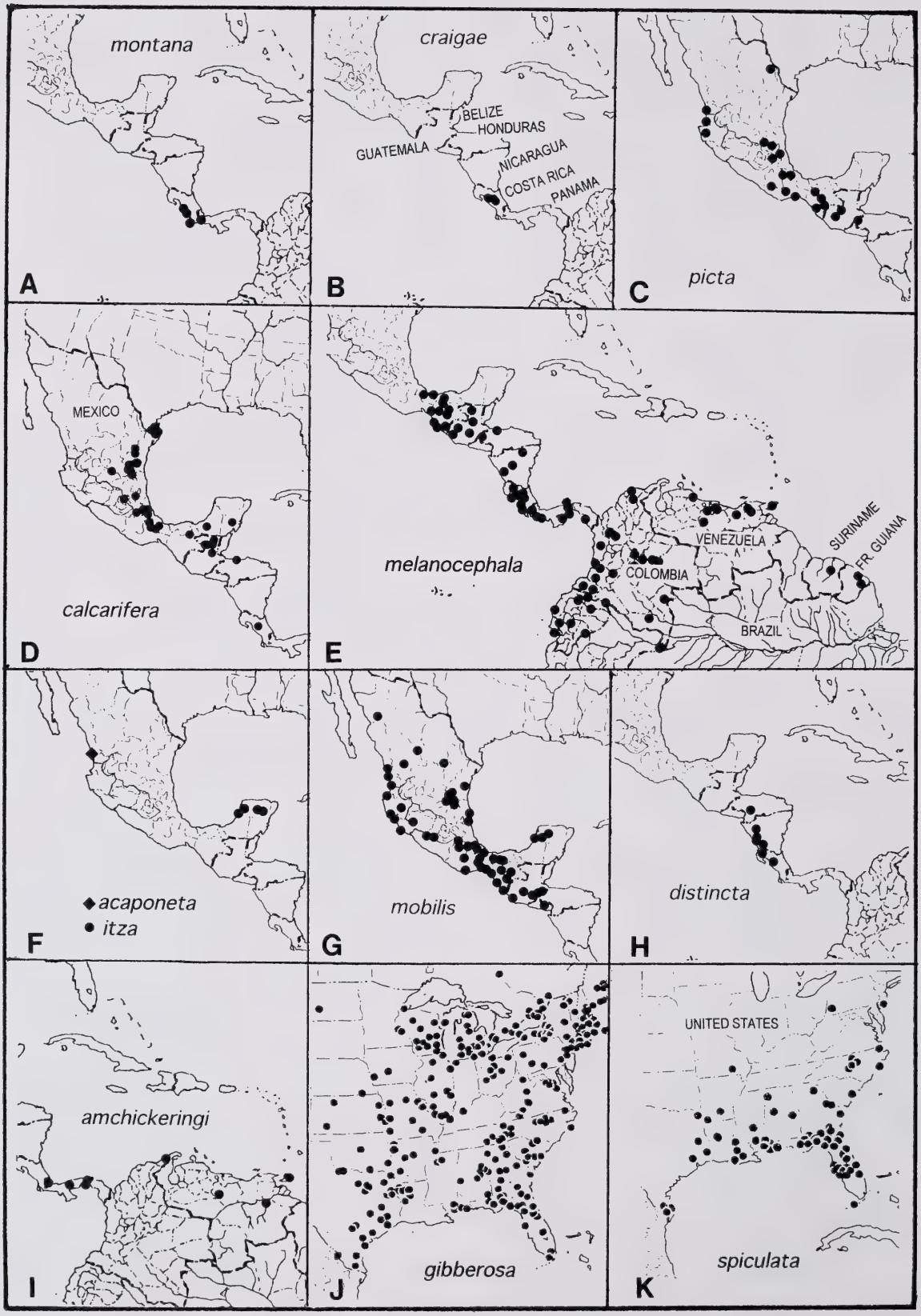
1	A black longitudinal line on venter of femora one and two (Fig. 100); abdomen dorsum with two or three lines (Figs. 93, 99)	2
–	Legs without black longitudinal lines; dorsum at times with lines	3
2(1)	In posterior view, epigynum with median plate upside-down T-shaped (Fig. 92); southeastern Canada to Tamaulipas (Map 1J)	*gibberosa*
–	Epigynum with median plate heart-shaped (Fig. 98); Mexico to Honduras, West Indies (Map 2A)	*fascialata*
3(1)	Abdomen with circular gray or black dots and/or posterior rectangles on whitish (in alcohol) dorsum (Figs. 139, 178, 185)	4
–	Without circular spots or posterior, black rectangles	12
4(3)	One pair of gray spots, plus black rectangles or bands on posterior of whitish (in alcohol) abdomen (Figs. 139, 143)	5
–	Abdomen with spots only or posterior black rectangles only (Figs. 178, 203)	6
5(4)	Epigynum with borders around lateral plates (Fig. 140); Chiapas (Map 2E)	*goodnightorum*
–	Epigynum with lateral plates indistinct (Fig. 136); Campeche (Map 2E)	*campeche*
6(4)	Abdomen dorsum with circular, black dots (Figs. 178, 185)	7
–	Abdomen without black dots, posterior with gray or black rectangles, sometimes pairs of lighter rectangles more anterior (Fig. 192)	8
7(6)	Abdomen dorsum with a series of black dots (Fig. 178); epigynum as in Figure 175; Yucatan Peninsula to Chiapas (Map 2H)	*chicanna*
–	Abdomen with only one pair of black dots (Fig. 185); epigynum as in Figure 182; Guatemala to Panama (Map 2H)	*purulha*
8(6)	Epigynum with a posterior, median, oval or angular notch (Figs. 193, 200)	9
–	Epigynum with a median posterior scape	10
9(8)	Notch oval with a median anterior tubercle (Fig. 193); central Mexico to Costa Rica (Map 2I)	*bimaculata*
–	Notch triangular (Fig. 200); Panama to northern South America (Map 2J)	*pia*
10(8)	Epigynum scape flanked by a semicircular notch on each side (Fig. 189); Costa Rica, Panama (Map 2H)	*schneirlai*

– No such notches present 11
11(10) Scape a semicircular, short lobe (Fig. 215); in posterior view, median plate flanked by narrow lateral plates (Fig. 216); Costa Rica (Map 2K) ..... *corcovado*
– Scape with base narrower than tip (Fig. 208); posterior median plate upside-down T-shaped (Fig. 209); Panama to Venezuela (Map 2K) ..... *falconae*
12(3) Abdomen (in alcohol) all white (Fig. 160), or with a median longitudinal white band flanked by darker lateral bands (Figs. 134, 147) 13
– Abdomen otherwise 15
13(12) Abdomen all white (Fig. 160); México, Michoacan (Map 2G) ..... *ixtapan*
– Abdomen with median band flanked by dark lateral bands (Figs. 134, 147) 14
14(13) Epigynum with a median oval scape (Fig. 131); Costa Rica, western Panama (Map 2D) ..... *fortuna*
– Epigynum with a small median posterior lobe (Fig. 144); Costa Rica (Map 2E) ..... *vito*
15(12) Venter of abdomen posterior to epigynum with a median patch with white pigment spots (Figs. 53, 61, 66, 153) 16
– Venter of abdomen behind epigynum without a median white patch 21
16(15) Abdomen dorsum with a pair of upside-down, comma-shaped marks on black (Fig. 152); epigynum as in Figures 148–151; Arizona to Nicaragua (Map 2F) ..... *passiva*
– Abdomen and epigynum otherwise 17
17(16) Posterior of epigynum with median plate longer than wide (Fig. 63); Mexico to Honduras (Map 1G) ..... *mobilis*
– Median plate wider than long (Figs. 50, 58) 18
18(17) Posterior median plate a narrow transverse band (Fig. 50); Yucatan Peninsula (Map 1F) ..... *itza*
– Posterior median plate not band-shaped (Figs. 58, 72, 81) 19
19(18) Posterior median plate with an anterior lobe on each side (Fig. 72); Honduras to Costa Rica (Map 1H) ..... *distincta*
– Median plate without anterior lobes (Figs. 58, 81) 20
20(19) Lateral plates in ventral view with a lateral, dark mark on median side of scape (Fig. 57); Nayarit (Map 1F) ..... *acaponeta*
– Lateral plates with dark marks anteriorly (Fig. 80); Costa Rica to northern South America (Map 1I) ..... *amchickeringi*
21(15) Epigynum with diagonal duct marks showing through cuticle on each side anterior to median depression (Figs. 20, 22); Texas to Costa Rica (Map 1D) ..... *calcarifera*
– Epigynum lacking these diagonal marks 22
22(21) Epigynum with a median scape or posterior lobe or sphere (Figs. 104, 110, 116, 121, 126, 164) 23
– Epigynum without scape or median lobe (Figs. 1, 8, 14, 30) 28
23(22) Scape flanked by large depressions (Fig. 164); Panama (Map 2G) ..... *candida*
– Epigynum lacking depressions next to scape 24
24(23) Scape flanked by diagonal sclerotized bars (Fig. 110); southeastern Canada to Nuevo Léon (Map 2B) ..... *placida*
– Epigynum otherwise 25
25(24) Scape flanked at some distance by curved, parallel bars (Fig. 104); eastern United States to probably Tamaulipas (Map 1K) ..... *spiculata*
– Epigynum otherwise 26
26(25) In posterior view, epigynum sclerotized, and lateral plates with a dorsal lobe (Fig. 117); Oaxaca (Map 2C) ..... *oaxaca*
– In posterior view, lightly sclerotized, lateral plates without a dorsal lobe (Figs. 122, 127) 27
27(26) In posterior view, median plate with a pair of ventral, lateral lobes (Fig. 122); México, Veracruz (Map 2C) ..... *nahuatl*
– Posterior median plate without lateral lobes (Fig. 127); western Panama (Map 2D) ..... *volcan*
28(22) Epigynum with indistinct median oval cavity, but with distinct, large, oval spermathecae, closer than their length from the margin (Fig. 14); Mexico to Honduras (Map 1C) ..... *picta*
– Epigynum otherwise 29
29(28) Spermathecae more than two diameters from posterior border and a flattened, posterior chevron, usually with a median notch or seam (Figs. 30, 34, 39); Veracruz to Brazil and Peru (Map 1E) ..... *melanocephala*
– Spermathecae closer to border, epigynum with different border (Figs. 1, 8) 30
30(29) Epigynum with a posterior, sclerotized, slightly wavy border (Fig. 8); Costa Rica (Map 1B) ..... *craigae*
– Epigynum with a straight border (Fig. 1); Costa Rica, Panama (Map 1A) ..... *montana*

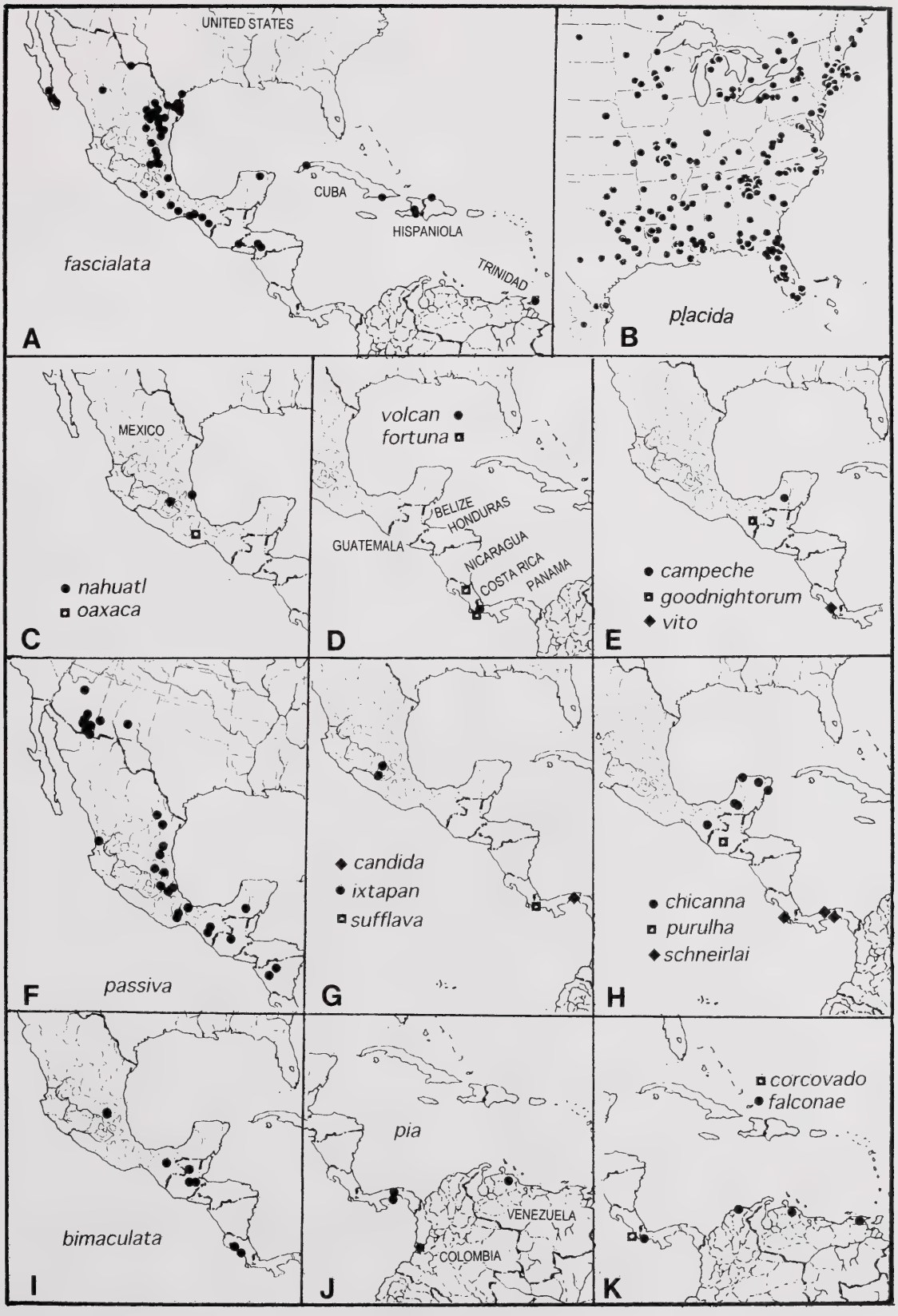
KEY TO MALE *MANGORA*

Males of nine species (*M. acaponeta, M. campeche, M. corcovado, M. fortuna, M. goodnightorum, M. nahuatl, M. oaxaca, M. schneirlai,* and *M. volcan*) are not known

1 A black longitudinal line on venter of



Map 1. Distribution of *Mangora* species.



Map 2. Distribution of *Mangora* species.

femora one and two (Fig. 100); abdomen dorsum with two or three lines (Figs. 93, 99) 2
– Legs without black longitudinal lines 3
2(1) Palpus in apical view with a blunt triangular projection (Fig. 96); southeastern Canada to Tamaulipas (Map 1J) ..... *gibberosa*
– Palpus, in apical view, with a wide band (Fig. 101); Mexico to Honduras, West Indies (Map 2A) ..... *fascialata*
3(1) Macroseta ventrally on proximal end of fourth femur (Figs. 47, 207) 4
– Without such macrosetae 6
4(3) Small size, less than 2.5 mm total length; palpus with filiform embolus (Figs. 43–45), Veracruz to Brazil and Peru (Map 1E) ..... *melanocephala*
– Large size, more than 3 mm total length; palpus otherwise, Panama to northern South America (Maps 2J, K) 5
5(4) Palpus, in apical view, with a sclerotized, wide thorn (Fig. 212) ..... *falconae*
– Palpus with only a small thorn (Fig. 204; Map 2J) ..... *pia*
6(3) Abdomen dorsum with black, circular spots or rectangles posteriorly (Figs. 178, 185, 192) 7
– Abdomen otherwise 10
7(6) Abdomen dorsum with black or gray circular dots (Figs. 178, 185) 8
– Abdomen with black or gray rectangles posteriorly (Fig. 192) 9
8(7) Abdomen dorsum with a series of pairs of dots (Fig. 178); palpus as in Figures 179–181; Yucatan Peninsula to Chiapas (Map 2H) ..... *chicanna*
– Abdomen dorsum with one pair of dots (Fig. 185); palpus as in Figures 186–188; Guatemala to Panama (Map 2H) ..... *purulha*
9(7) Palpus, in apical view, with sickle-shaped structure (Fig. 197); central Mexico to Costa Rica (Map 2I) ..... *bimaculata*
– Palpus, in apical view, with drawn-out point (Fig. 173); western Panama (Map 2G) ..... *sufflava*
10(6) Left palpus, in apical view, showing embolus with counterclockwise filament (Figs. 5, 11, 17, 26) 11
– Apical view otherwise 14
11(10) Embolus turns clockwise before reversing direction (Fig. 26); Texas to Costa Rica (Map 1D) ..... *calcarifera*
– Embolus turns only counterclockwise (Figs. 5, 11, 17) 12
12(11) Terminal apophysis, in apical view, with single, large, sclerotized thorn adjacent to a truncate tip (Fig. 11); Costa Rica ..... *craigae*
– Terminal apophysis with only thorn or only truncate tip 13
13(12) Terminal apophysis, in apical view, with only a thorn (Fig. 5); Costa Rica, Panama (Map 1A) ..... *montana*
– Terminal apophysis, in apical view, with only a truncate tip (Fig. 17); Mexico to Honduras (Map 1C) ..... *picta*
14(10) Terminal apophysis, in apical view, with a sclerotized, pointed rod (Figs. 67, 76, 85, 89, 154) 15
– Terminal apophysis otherwise 20
15(14) Rod sword-shaped with one straight and one curved edge (Fig. 154); Arizona to Nicaragua (Map 2F) ..... *passiva*
– Terminal apophysis tip otherwise 16
16(15) Rod with right angle (Fig. 161); México, Michoacan (Map 2G) ..... *ixtapan*
– Rod otherwise (Fig. 168) 17
17(16) Sword-shaped rod with both sides evenly curved (Fig. 168); Panama (Map 2G) ..... *candida*
– Terminal rod first curved in one direction, distally in another (Figs. 67, 76, 85) 18
18(17) In mesal view, median apophysis with evenly curved "top" (Fig. 79); Honduras to Costa Rica (Map 1H) ..... *distincta*
– Median apophysis "top" not so curved (Figs. 70, 88) 19
19(18) Both spines of median apophysis almost equal in size; "top" flattened (Fig. 88); Costa Rica to northern South America (Map 1I) ..... *amchickeringi*
– One spine much larger than other; "top" skewed (Fig. 70); México to Honduras (Map 1G) ..... *mobilis*
20(14) Terminal apophysis, in apical view, with thorn and lobe, separated by a notch as in Figure 54; Yucatan Peninsula (Map 1F) ..... *itza*
– Terminal apophysis otherwise (Figs. 107, 113) 21
21(20) Median apophysis with two spines (6h in Fig. 108); southeastern Canada to Nueva Léon (Map 1K) ..... *spiculata*
– Median apophysis with one spine (6 h in Fig. 114); eastern United States to Nuevo Léon (Map 2B) ..... *placida*

Mangora montana Chickering
Figures 1–7; Map 1A

Mangora montana Chickering, 1954: 204, figs. 15–17, ♀♂. Male holotype and female allotype from El Volcán, Panama, in MCZ, examined. Platnick, 2004.

Description. Female paratype from El Volcán. Carapace, legs, sternum grayish orange-white. Abdomen dorsum with

black, gray, and white pigment spots (Fig. 3); venter well marked (Fig. 4). Posterior eye row procurved. Ocular trapezoid longer than wide, widest posteriorly. Posterior median eyes 1.5 diameters of anterior medians; lateral eyes 0.8 diameter. Anterior median eyes 0.9 diameter apart, 0.9 from laterals. Posterior median eyes 0.7 diameter apart, 0.7 from laterals. Total length 3.4 mm. Carapace 1.5 mm long, 1.1 wide in thoracic region, 0.7 wide behind eyes, 0.7 high. First femur 1.4 mm, patella and tibia 1.7, metatarsus 1.4, tarsus 0.7. Second patella and tibia 1.7 mm, third 1.0, fourth 1.6.

Male from Osa Peninsula, Costa Rica. Lighter than female, with only faint coloration on dorsum of abdomen. Posterior eye row procurved. The median eye trapezoid is longer than wide, slightly wider posteriorly. Posterior median eyes 1.3 diameters of anterior medians; lateral eyes 0.6 diameter. Anterior median eyes 0.8 diameter apart, 0.8 from laterals. Posterior median eyes 0.4 diameter apart, 0.4 from laterals. Height of clypeus 1.5 diameters of anterior median eye. Total length 2.3 mm. Carapace 1.3 mm long, 1.0 wide in thoracic region, 0.4 wide behind lateral eyes, 0.7 high. First femur 1.3 mm, patella and tibia 1.4, metatarsus 1.2, tarsus 0.6. Second patella and tibia 1.2 mm, third 0.7, fourth 1.2.

Variation. Total length of females 2.6–3.6 mm, males 2.1–2.6 mm. The illustrations were made from female paratypes and males from El Volcán, Panama.

Diagnosis. Mangora montana is darker (Figs. 3, 4) than *M. craigae* (Fig. 10), and the epigynum has a sclerotized, almost posterior straight edge (Fig. 1), whereas that of *M. craigae* is less sclerotized (Fig. 8) and the posterior edge has slight dents (Figs. 8, 9).

The male is distinguished from that of *M. craigae* by a differently shaped terminal apophysis (compare 12 h in Figs. 5–7 and 12 h in Figs. 11–13).

Distribution. Costa Rica, western Panama (Map 1A).

Paratypes. PANAMA *Chiriquí*: Boquete, July 1939, 1♀ (A. M. Chickering, MCZ); El Volcán, 20 Feb. 1936, many ♀♂ (W. J. Gertsch, AMNH); Aug. 1950, 2♀ (A. M. Chickering, MCZ); Cerro Punta, 3 Feb. 1936, 1♀ (W. J. Gertsch, AMNH).

Specimens Examined. COSTA RICA *Puntarenas*: Butler's Finca, 9°15′N, 83°47′W, 28 Jan. 1976, 2♀ (Roth-Schropfer, AMNH); San Isidro del General, 660–1,300 m, 2♀ (D. Round, MCZ); Osa Peninsula, 4 km SW Rincón, 08°42′N, 83°29′W, Feb. 1967, 1♂ (Organization for Tropical Studies, MCZ).

Mangora craigae new species
Figures 8–13; Map 1B

Holotype. Male holotype from Monteverde Cloud Forest, Bosque del Río, 1,580 m, Puntarenas Province, Costa Rica, 13 July 1977, female paratype, 4 Aug. 1977 (C. L. Craig) in MCZ. The species is named after the collector, arachnologist Cay Craig.

Description. Female paratype. Prosoma orange, with legs lighter. Abdomen orange-white with a pair of dorsal, longitudinal bands of white spots (Fig. 10), sides with similar bands, joining anteriorly; venter with bands between epigynum and spinnerets. Posterior eye row procurved. Ocular trapezoid longer than wide, widest posteriorly. Posterior median eyes 1.3 diameters of anterior medians; anterior lateral eyes 1.0 diameter, posterior laterals 0.7. Anterior median eyes their diameter apart, 1.0 diameter from laterals. Posterior median eyes their diameter apart, 1.0 diameter from laterals. Total length 3.5 mm. Carapace 1.6 mm long, 1.3 wide in thoracic region, 0.7 wide behind eyes, 0.8 high. First femur 1.7 mm, patella and tibia 1.8, metatarsus 1.7, tarsus 0.8. Second patella and tibia 1.7 mm, third 1.3, fourth 1.7.

Male holotype. Lighter than female. Eye arrangement similar to that of female. Posterior median eyes 1.0 diameter of anterior medians; lateral eyes 0.6 diameter. Anterior median eyes 1.0 diameter apart, 0.8 from laterals. Posterior median eyes 0.8 diameter apart, 0.8 from laterals. Total length 2.7 mm. Carapace 1.4 mm long, 1.2 wide in thoracic region, 0.5 wide behind eyes, 0.8 high. First femur 1.5 mm, patella and tibia 1.6, metatarsus 1.3, tarsus 0.7.

Second patella and tibia 1.5 mm, third 0.8, fourth 1.5.

Variation. Total length of females 2.8–3.8 mm, males 2.6–2.7 mm. The illustrations were made from female paratypes, and male from the holotype.

Diagnosis. Mangora craigae is lighter than *M. montana* and has the epigynum lightly sclerotized with an undulating posterior edge (Fig. 8), unlike that of *M. montana* (Fig. 1); in posterior view the median plate is smaller (Fig. 9) than that of *M. montana.*

In the palpus of the male, the terminal apophysis (12 h in Figs. 11–13) is different in shape from that of *M. montana* (Figs. 5–7).

Natural History. Specimens have been found in cloud forest at Monteverde, and roadside in forest in Braulio Carrillo National Park.

Distribution. Costa Rica (Map 1B).

Paratypes. COSTA RICA *Cartago* [?]: Orosi ["central flat land," Reimoser, 1940], 1♀ (Picado, MCZ). *San José*: Braulio Carrillo Natl. Park, 1,400–1,600 m, 26 July 1983, 2♀ (H., L. Levi, W. Eberhard, MCZ); Bajo Hondura, 1,250 m, Mar. 1986, 3♀; 26 July 1983, 3♀; Dec. 1989, 2♀ (W. Eberhard, MCZ); Río Hondura, 30 Mar. 1991, 1,200 m, 2♀ (W. Eberhard, MCZ); Zurqui, 1,600 m, May 1992, 1♂ (W. Eberhard, MCZ). *Alajuela*: Peñas Blancas, headwaters of Río Peñas Blancas, 13 July 1980, 1♀ (J. Coddington, MCZ). *Puntarenas*: Monteverde Biol. Reserve, 17 Mar. 1979, 1♀; 3 Apr. 1979, 1♂; 5 June 1980, 1♀ (J. Coddington, MCZ, USNM); Bosque del Río, 1 May 1977, 1♀; 11 May 1977, 1♀; 3 July 1977, 1♀; 23 July 1977, 1♀; 3 Aug. 1977, 1♀; 24 May 1978, 1♂ (C. L. Craig, MCZ); Bosque Nuboso, 22 July 1978, 1♀ (C. L. Craig, P. Klass, MCZ); Las Cruces nr. San Vito, 1,100 m, Jan. 1987, 2♀ (W. Eberhard, MCZ).

Mangora picta O. P.-Cambridge
Figures 14–19; Map 1C

Mangora picta O. P.-Cambridge, 1889: 14, pl. 3, fig. 5, ♂. Male lectotype here designated from Chactum [?], Guatemala in BMNH, examined. F. P.-Cambridge, 1904: 479, pl. 45, fig. 14, ♂. Platnick, 2004.

Mangora trilineata O. P.-Cambridge, 1889: 14, pl. 3, fig. 7, ♀. Female lectotypes, here designated from Chiacam [coffee plantation, Alta Verapaz, 26 km NE Cobán (Selander and Vaurie, 1962)], Guatemala, in BMNH, examined. F. O. P.-Cambridge, 1904: 480; pl. 45, fig. 20, ♀. Chickering, 1954: 213, figs. 27, 28, ♀. Platnick, 2004. NEW SYNONYMY.

Note. Chickering (1954) noted, correctly, that the female described with *Mangora picta* is actually the female of *M. melanocephala* (=*M. spinula*), but overlooked the correct match of the female of *M. trilineata* with the male of *M. picta.* Males and females are commonly collected together.

Description. Female from Xilitla, San Luis Potosí, Mexico. Carapace orange, with a dusky patch on each side of thoracic region. Legs light orange. Abdomen orange-white, with posterior median black ladder, and areas with white pigment spots (Fig. 16); venter orange-white. Posterior eye row procurved. Ocular trapezoid longer than wide, widest posteriorly. Posterior median eyes 1.5 diameters of anterior medians; lateral eyes 0.7 diameter. Anterior median eyes 0.6 diameter apart, 0.6 from laterals. Posterior median eyes 0.4 diameter apart, 0.5 from laterals. Total length 2.7 mm. Carapace 1.2 mm long, 1.0 wide in thoracic region, 0.5 wide behind eyes, 0.7 high. First femur 1.5 mm, patella and tibia 1.7, metatarsus 1.4, tarsus 0.6. Second patella and tibia 1.5 mm, third 0.9, fourth 1.7.

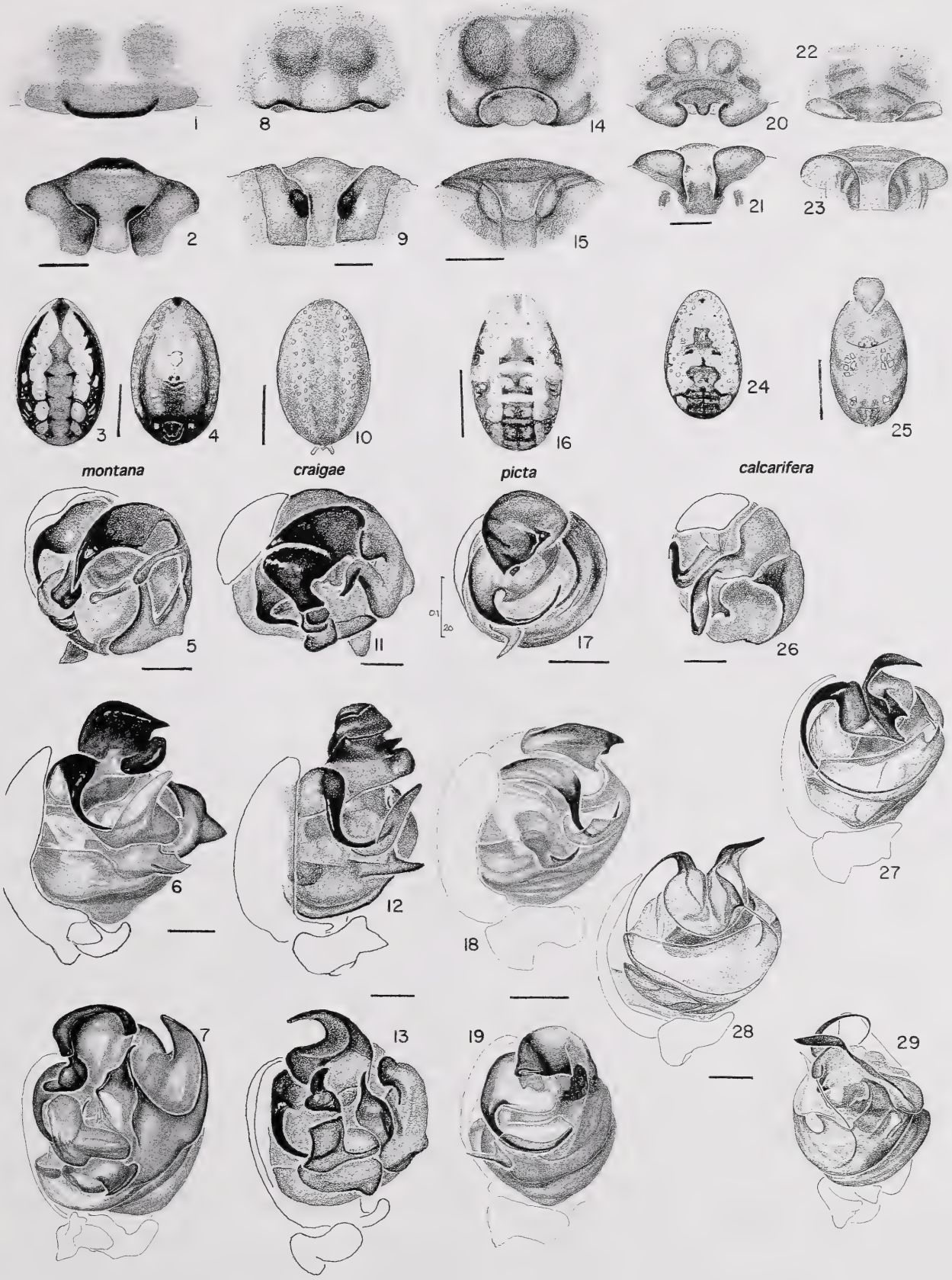
Male lighter than female. Posterior median eyes 1.5 diameters of anterior medians; lateral eyes 0.7 diameter. Anterior median eyes 1.0 diameter apart, 0.8 from laterals. Posterior median eyes 1.3 diameters apart, 0.8 from laterals. Total length 1.8

→

Figures 1–7. *Mangora montana* Chickering. 1–4, female. 1, 2, epigynum. 1, ventral. 2, posterior. 3, abdomen, dorsal. 4, abdomen, ventral. 5–7, male, left palpus. 5, apical. 6, mesal. 7, ventral.

Figures 8–13. *Mangora craigae* new species. 8–10, female. 8, 9, epigynum. 8, ventral. 9, posterior. 10, abdomen, dorsal. 11–13, male, palpus. 11, apical. 12, mesal. 13, ventral.

Figures 14–19. *Mangora picta* O. P.-Cambridge. 14–16, female. 14, 15, epigynum. 14, ventral. 15, posterior. 16, abdomen, dorsal. 17–19, male, palpus. 17, apical. 18, mesal. 19, ventral.



Figures 20–29. *Mangora calcarifera* F. O. P.-Cambridge. 20–25, female. 20–23, epigynum. 20, 22, ventral. 21, 23, posterior. 24, abdomen, dorsal. 25, abdomen, ventral. 26–29, male, palpus. 26, apical. 27, mesal. 28, ventral. 29, lateral.

Scale lines: 1.0 mm, genitalia 0.1 mm.

mm. Carapace 1.1 mm long, 0.9 wide in thoracic region, 0.4 wide behind eyes, 0.6 high. First femur 1.2 mm, patella and tibia 1.5, metatarsus 1.2, tarsus 0.7. Second patella and tibia 1.4 mm, third 0.8, fourth 1.3.

Variation. Total length of females 2.5–3.4 mm, males 1.8–2.4 mm. The illustrations were made from the female lectotypes of *M. trilineata,* and from the male lectotype of *M. picta.*

Diagnosis. The epigynum of *M. picta* is lightly sclerotized; the depression is variable in shape, and the rim barely distinct. It is distinguished from all other species by the large, distinct pair of seminal receptacles, less than their length from the posterior edge (Fig. 14).

Males have a distinct terminal apophysis (12 h in Figs. 17–19) differing from that of *M. montana* (Figs. 5–7) and *M. craigae* (Figs. 11–13).

Natural History. Specimens have been collected from a bromeliad at Fortín, Veracruz, and from tropical, deciduous forest in Jalisco, Mexico.

Distribution. Nuevo Léon, Mexico to western Honduras (Map 1C).

Specimens Examined. MEXICO *Nuevo Léon*: Tierran, 20 km NW Laredo, 27 July 1945, 1♀ (H. Wagner, AMNH). *San Luis Potosí*: Fortín, 25 July 1956, 1♀, 2♂ (V. Roth, AMNH); 26 June 1944, 2♀ (L. I. Davis, AMNH); 3.2 km N Fortín, 5♀, 3♂ (J., W. Ivie, AMNH); Huachinango, 7 Oct. 1947, 1♀ (H. M. Wagner, AMNH); Huichichuyan, 19 May 1952, many ♀♂ (W. J. Gertsch, AMNH); Picolo, 21 May 1952, 1♀ (W. J. Gertsch et al., AMNH); Tamazunchale, 6, 7 July 1941, 1♀ (A. M., L. I. Davis, AMNH); 23 Nov. 1946, 1♀ (CAS); 20 May 1952, 1♀, 1♂ (W. J. Gertsch, AMNH); 19 Apr. 1963, 1♀ (W. J. Gertsch, W. Ivie, AMNH); Valles, 1961, 1♀ (L. Steude, AMNH); 13 km NNW Xilitla, 23 July 1954, 1♀, 2♂ (R. Dreisbach, MCZ); Xilitra, 16 km NE Xilitla, 19 Apr. 1963, 1♀ (W. J. Gertch, W. Ivie, AMNH); Cueva de Salitre, ca. 21°23′N, 98°23′W, 13 June 1983, 1♀ (W. Maddison, MCZ). *Nayarit*: Compostela, 16 Sep. 1957, 1♀ (R. Dreisbach, MCZ); Tepic, 22–24 Sep. 1947, 2♀ (B. Malkin, AMNH); 30 km SW Río Cañas, 4 Nov. 1987, 1♀ (V. F. Lee, CAS). *Jalisco*: Municipio El Limón, 3 Sep. 1997, 1♀ (F. Alvarez, MCZ); 26 km S Autlan, 8 July 1984, 1♀ (J. Woolley, AD); Esta. Biol. Chamela, 100 m, Sep. 1987, 1♀ (W. Eberhard, MCZ). *Colima*: 14 km N Comala, 12 July 1984, 2♂ (J. Woolley, AD). *Veracruz*: Córdoba, 1909, 4♀, 1♂ (A. Petrunkevitch, AMNH); 13–15 May 1946, 4♀ (J. C., D. L. Pallister, AMNH); 3.2 km E Córdoba, 6 Aug. 1966, 1♀ (J., W. Ivie, AMNH); Fortín, 20 May 1947, 1♀ (Bordas, AMNH); 5 Aug. 1966, many ♀♂ (J., W. Ivie, AMNH); 4.2 km NE Huatusco, 22 July 1985, many ♀♂ (J. Woolley et al., AD); Jalapa, 22 May 1946, many ♀♂ (J. C., D. L. Pallister, AMNH); Roma nr. Jalapa, Aug. 1948, 1♂ (C., M. Goodnight, AMNH); July 1981, 3♀, 1♂ (C. Gold, CAS); La Planta de Moctezuma, nr. Fortín; 7 July 1947, 1♀ (C., M. Goodnight, AMNH); 17 Dec. 1948, 1♀ (H. B. Leech, CAS); Mirador, Zacuapam, 20 Aug. 1933, 1♀ (W. James, AMNH); Orizaba, 12 Feb. 1954, 1♀ (R. R. Dreisbach, MCZ); Penuela, 18°53′N, 96°48′W, 26 Apr. 1963, 1♀ (W. J. Gertsch, W. Ivie, AMNH); Potrero, 24 June 1936, 1♀ (L. I. Davis, AMNH); Tlapacoyan, 300 m, 7–8 July 1946, 1♀ (H. Wagner, AMNH); 24 June 1947, 2♀, 1♂ (L. I. Davis, AMNH). *Hidalgo*: Chapulhuacan, 20 May 1952, 1♀ (W. J. Gertsch et al., AMNH); 27 July 1966, 1♀ (J., W. Ivie, AMNH). *Puebla*: Huauchinango, 7 Oct. 1947, many ♀♂ (H. Wagner, AMNH); Villa Juarez, 10 Oct. 1947, many ♀♂ (H. Wagner, AMNH); 1.5 km. W of Hwy. 130, bypass of Xicotepec de Juarez, ca. 20°17′N, 97°59′W, 17 June 1983, 1♂ (W. Maddison, MCZ); 7.5 km. SW La Cumbre, 1,730 m, 23 July 1987, 3♀, 4♂ (Kopvarik, Schaffner, AD); 6.2 km NE San Gabriel Mixtepec, 16 July 1985, 1♀ (J. Woolley, AD). *Guerrero*: 3.2 km E Ocotito, 11 July 1985, 1♂ (J. Woolley et al., AD). *Oaxaca*: 7.5 km S San Gabriel Mixtepec, 16 July 1985, 2♂ (J. Woolley et al., AD); 30.4 km S San Miguel Suchixtepec, 17 July 1985, 1♀ (J. Woolley, AD); Soledad, 7 May 1947, 1♀ (H. Wagner, AMNH); Porto Escondido, 15 July 1985, 2♂ (J. Woolley et al., AD); 12.8 km NE El Punto, 18 July 1985, 1♂ (J. Woolley et al., AD). *Chiapas*: Finca Cuauhtemoc nr. Cacahuatan, 3–13 Aug. 1950, 2♀, 2♂ (C., M. Goodnight, AMNH); Finca Cusuhtemoc, 6 Aug. 1950, 1♀ (C. Goodnight, AMNH); Finca Lubeca, 20 km N Huixtla, 11 Jan. 1945, 2♀, 1♂ (T. C. Schneirla, AMNH); Lagunas de Montebello, 48 km Comitan, 23 Aug. 1977, 4♀, 1♂ (T. C. Meikle, C. E. Griswold, CAS); Ocosingo, 24, 25 June 1950, 1♀, 1♂ (C., M. Goodnight et al., AMNH); rim of canyon 5 km S Sumidero, 16°48′N, 93°05′W, 17 Aug. 1966, 1♀ (J., W. Ivie, AMNH). GUATEMALA Yepocapa, Chimaltenango, 30 Aug. 1948, 1♀ (H. T. Dalmat, USNM); 1,400 m, 27 July 1949, 2♂ (T. H. Farr, AMNH); Mocá, June 1947, many ♀♂; 31 Aug. 1947, 1♀ (C., P. Vaurie, AMNH); Tumahu, 1,000 m, 10–11 July 1947, 2♀ (C., P. Vaurie, AMNH). *Quixchaya*: Suchitepequez, 9 Oct. 1944, 1♂ (H. Elishewitz, AMNH). HONDURAS *Copán*: Copán, 16 Feb. 1937, sweeping weeds, 1♀ (Roys, MCZ).

Mangora calcarifera F. O. P.-Cambridge
Figures 20–29; Map 1D

Mangora calcarifera F. O. P.-Cambridge, 1904: 479, pl. 45, figs. 12, 13, ♀♂. Two female, two male syntypes from Petexbatún, Guatemala, in BMNH, ex-

amined. Levi, 1975: 132, figs. 131–144. Platnick, 2004.

Description. Description is found in Levi (1975).

Variation. Total length of females 3.2–4.4 mm, males 2.2–2.7 mm.

Diagnosis. The epigynum of *M. calcarifera* is lightly sclerotized and variable; it is distinguished from that of other species by the one or two pairs of diagonal marks made by ducts that show through the transparent cuticle, anterolateral to the median depression (Figs. 20, 22). Unlike other species with a lightly sclerotized epigynum, in *M. calcarifera* the venter of the abdomen has two pairs of areas containing silver spots (Fig. 25).

The male has a longer filamentous embolus in the palpus (Figs. 27, 28) than have other Mexican and Central American *Mangora,* and has a distinct distal flap like a rabbit's ear on the tip of the palpus (Figs. 26–29), similar to the palpus of *M. melanocephala* (Fig. 45). However, the male lacks the macroseta on the fourth femur present in the male of *M. melanocephala* (Fig. 47).

Natural History. A specimen was found in deep weeds at Salto Falls, San Luis Potosí.

Distribution. Texas to Costa Rica, mostly in eastern regions, the Gulf drainage (Map 1D).

Specimens Examined. TEXAS *Cameron Co.*: 16 km SE Brownsville, 8 Oct. 1937, 1♀ (Davis, Fones, MCZ). MEXICO *Tamaulipas*: 1 km N Gomez Farias, 26 Dec. 1971, 2♀ (C. J. Durden, USNM); 51 km S Ciudad Victoria, 29 Jan. 1947, 1♀ (AMNH). *San Luis Potosí*: 10 km N Naranjo Salto, 5 May 1973, 1♂ (B. Vogel, USNM); nr. Ciudad del Maiz, 760 km, 28 July 1953, 1♀ (C. J. Goodnight, AMNH); Huichichuyan, 19 May 1952, 2♀ (W. J. Gertsch, AMNH); Salto Falls, 5 Feb. 1967, 1♀ (W. Peck, CAS); Tamanzuchale, 15 Apr. 1946, 2♀ (L. Davis, M. Johnston, AMNH); 20 May 1952, 1♂ (W. J. Gertsch et al., AMNH); 20 July 1956, 1♂ (W. J. Gertsch, V. Roth, AMNH); 1.6 km SW Tamazunchale, 25 July 1966, 1♀ (J., W. Ivie, AMNH); Xilitla, 23 July 1954, 1♂ (R. Dreisbach, MCZ); 16 km NE Xilitla, 19 Apr. 1963, 1♂ (W. J. Gertsch, W. Ivie, AMNH); Valles, 1961, 2♀, 1♂ (L. Steude, AMNH). *Veracruz*: Catemaco, Playa Azul, 9 Aug. 1966, 1♀, 1♂ (J., W. Ivie, AMNH); 7.5 km W of Catemaco, 23 June 1982, 1♀ (F. Coyle, MCZ); 4 km E Huatusco, 23 July 1984, 1♀ (J. B. Woolley, AD); nr. La Palma, N of Catemaco, 18°36′N, 95°07′W, 29 June–1 July 1983, 2♀; 1, 2 Aug. 1983, 2♀ (W. Maddison, MCZ); Jesus Carranza, 13 July 1947, 1♀ (C. Goodnight, AMNH); Los Tuxtlas Biol. Sta., July 1990, 1♀ (B. Traw, MCZ); Martínez de la Torre, 4 July 1946, 1♂ (H. Wagner, AMNH); Papantla, 12 Oct. 1947, 2♂ (H. Wagner, AMNH); Poza Rica, 13 Apr. 1946, 1♀ (C. Bolivar, AMNH); Tecolutla, 13 Oct. 1947, 1♀ (H. Wagner, AMNH); Tlapacoyan, 300 m, 1, 8 July 1946, 1♂ (H. Wagner, AMNH). *Hidalgo*: SW Progreso, March 1936, 1♀, 1♂ (L. I. Davis, AMNH). *Puebla*: Huachinango, 7 Oct. 1947, 1♀, 2♂ (H. M. Wagner, MCZ). *Oaxaca*: Tolosa, 1–12 Apr. 1947, 1♀ (B. Malkin, AMNH). *Campeche*: 6 km W Francisco Escarcegan, 18°37′N, 90°48′W, 11, 12 July 1983, 1♀ (W. Maddison, MCZ). *Quintana Roo*: 31 km NE of Felipe Carrillo, 19°48′N, 87°52′W, 17 July 1983, 2♀ (W. Maddison, MCZ). *Chiapas*: Palenque Ruins, 9 July 1949, 1♂ (C. Goodnight, AMNH); Ocosingo, 900 m, 24, 25 June 1950, 1♀, 2♂ (C., M. Goodnight et al., AMNH). GUATEMALA *Petén*: Tikal, 7 July 1975, 1♂ (W. Sedgwick, MCZ); Uaxactún, Mar., Apr. 1931, 1♀ (H. H. Bartlett, MCZ). HONDURAS nr. Lancetilla, 19 July 1929, 1♂ (A. M. Chickering, MCZ). COSTA RICA *San José*: Cerro Zurqui, 1,600 m, May 1992, 1♀ (W. Eberhard, MCZ).

Mangora melanocephala (Taczanowski)
Figures 30–47; Map 1E

Linyphia melanocephala Taczanowski, 1874: 70. Male and female syntypes from Cayenne, French Guiana, in PAN, examined.

Zilla melanocephala:—Keyserling, 1881: 552, pl. 16, fig. 4, ♀♂; 1893: 302, pl. 15, fig. 223, ♀♂.

Mangora picta:—O. P.-Cambridge, 1889: 14, pl. 3, fig. 6, ♀; F. O. P.-Cambridge, 1904: 479, pl. 45, ♀ (female only, not male holotype). Error first reported by Chickering, 1954.

Mangora spinula F. O. P.-Cambridge, 1904: 480, pl. 45, fig. 18, ♂. Male holotype from Teapa, [Tabasco], Mexico, in BMNH, examined. Chickering, 1954: 211, figs. 23–26, ♀. Platnick, 2004. NEW SYNONYMY.

Mangora dentembolus Chamberlin and Ivie, 1936: 59, pl. 12, figs. 114–116, ♂. Male holotype from Barro Colorado Island, Panama, vial present in AMNH, but specimen lost. Synonymized with *spinula* by Chickering, 1954. NEW SYNONYMY.

Zygiella melanocephala:—Roewer, 1942: 887.

Mangora aragarcensis Soares and Camargo, 1948: 372, figs. 27, 28, ♀. Female holotype from Aragarças, Goiás, Brazil, in MZSP no. 1215, examined. Platnick, 2004. NEW SYNONYMY.

Mangora melanocephala:—Caporiacco, 1948: 659. Platnick, 2004. Caporiacco first recognized that *Linyphia melanocephala* is a *Mangora.*

Mangora pozonae Schenkel, 1953: 20, fig. 18, ♀. Female holotype from Conwarook (Potaro), Pozón,

Depto. Acosta, Falcón, Venezuela, in NMB, examined. Platnick, 2004. NEW SYNONYMY.

Note. Keyserling (1881) had apparently examined the original specimens of Taczanowski and made good illustrations of the genitalia, which had been ignored.

Description. Female from Panama. Prosoma orange, with a dusky patch on each side of thoracic region of carapace (Fig. 38), legs lighter. Abdomen orange-white, with posterior median black ladder, and areas with white pigment spots (Fig. 38); venter orange-white. Posterior eye row procurved. Ocular trapezoid longer than wide, widest posteriorly. Posterior median eyes 1.5 diameters of anterior medians; lateral eyes 0.7 diameter. Anterior median eyes 0.6 diameter apart, 0.6 from laterals. Posterior median eyes 0.4 diameter apart, 0.5 from laterals. Total length 2.7 mm. Carapace 1.2 mm long, 1.0 wide in thoracic region, 0.6 wide behind eyes, 0.7 high. First femur 1.5 mm, patella and tibia 1.7, metatarsus 1.4, tarsus 0.6. Second patella and tibia 1.5 mm, third 0.9, fourth 1.7.

Male from Panama lighter than female. Posterior median eyes 1.3 diameters of anterior medians; lateral eyes 0.8 diameter. Anterior median eyes 1.0 their diameter apart, 0.8 from laterals. Posterior median eyes 1.3 diameters apart, 0.8 from laterals. Total length 1.8 mm. Carapace 1.1 mm long, 0.9 wide in thoracic region, 0.4 wide behind eyes, 0.6 high. First femur 1.2 mm, patella and tibia 1.5, metatarsus 1.2, tarsus 0.7. Second patella and tibia 1.4 mm, third 0.8, fourth 1.3.

Variation. Total length of females from Central America 2.3–3.5 mm, males 1.7–2.1 mm. The epigynum is lightly sclerotized and the posterior rim quite variable (Figs. 30, 34, 39); the posterior swelling varies in angles and in thickness; in posterior view the median borders of the lateral plates are usually, but not always, parallel and close to each other (Figs. 31, 35).

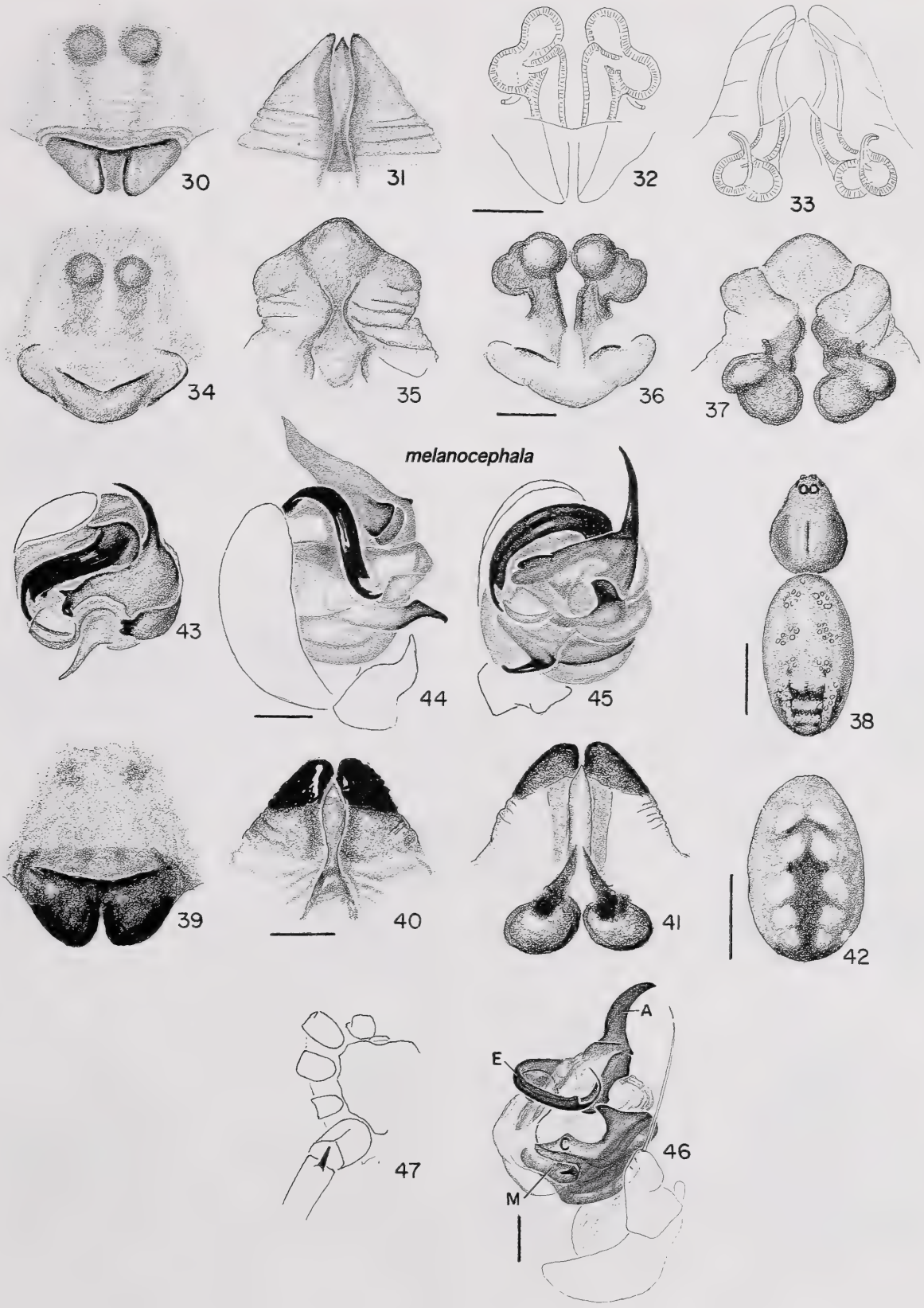
Diagnosis. The epigynum of *M. melanocephala* is lightly sclerotized and distinguished from that of other *Mangora* in the region by having the spherical spermathecae of the epigynum placed far anterior from the chevron-shaped posterior swelling (Figs. 30, 34); the swelling is variable in thickness and shape, rarely sclerotized (Fig. 30). The median plate, in posterior view, is narrow and bordered by parallel edges of the lateral plates (Fig. 31).

Males are the only tiny (1.7–2.1 mm) *Mangora* in Central America with a macroseta on the ventral face of the fourth femur (Fig. 47); the others with macroseta on the fourth femur are the larger-sized *M. pia* and *M. falconae.* Another distinctive character is the projection on the terminal apophysis of the palpus, and the ragged-tipped embolus (Figs. 43–46).

Natural History. The species has been collected in various habitats: river bottom; in lowland forest south of Volcán, Costa Rica; in understory of secondary forest, in open vegetation and cultivated areas at La Selva, Costa Rica; in low vegetation, forest edge and low vegetation, dense jungle near Turrialba, Costa Rica; in vegetation along ditch at Finca la Laja Forest in Costa Rica. Also, it has been found as prey of *Trypoxylon saussurei* wasps in Costa Rica (no locality, R. Coville collection) and canopy fogging of monsoon forest in Panama City and humid forest in Colón.

Distribution. From the Isthmus of Tehuantepec to Peru and Brazil (Map 1E). (Additional South American records will be published in a separate paper.)

Specimens Examined. MEXICO *Veracruz*: 61 km S Acayucan, 17°57′N, 94°54′W, 2 March 1976, ♀ (V. Roth, AMNH); Catemaco, 9 Aug. 1966, ♀♂ (J., W. Ivie, AMNH); La Buena Ventura, July 1909, ♀♂ (A. Petrunkevitch, AMNH); 16 km S San José del Carmen, 16 Apr. 1953, ♂ (L. I. Davis, AMNH). *Chiapas*: Cacahuatan, 9 Aug. 1950, ♀ (C., M. Goodnight, AMNH); El Real, 6, 7 July 1950, ♀ (C., M. Goodnight, AMNH); Escuintla, ♀♂ (N. Banks, MCZ); Finca Santa Marta, nr. Huehuetan, 31 July–1 Aug. 1950, ♀ (C., M. Goodnight, AMNH); Ocosingo, 900 m, 25 June 1950, ♂ (C., M. Goodnight et al., AMNH); Las Ruinas Palenque, July 1948, ♀♂ (C., M. Goodnight, AMNH); 22 July 1949, ♂ (C. Goodnight, AMNH); Pichuacalco, 17 July 1947, ♀ (C. J. Goodnight, AMNH); La Zacualpa, Aug. 1909, ♀♂ (A.



Figures 30–47. *Mangora melanocephala* (Taczanowski). 30–42, female. 30–37, 39–41, epigynum. 30, 34, 39, ventral. 31, 35, 40, posterior. 32, 36, ventral cleared. 33, 37, 41, posterior, cleared. 30–34, syntype. 35–37, Costa Rica, unusual specimen. 38, carapace and abdomen. 39–42, Nicaragua, doubtful determination. 42, abdomen, dorsal. 43–46, male, left palpus. 43, apical. 44, mesal. 45, ventral. 46, left palpus, expanded. 47, macroseta on fourth femur.

Scale lines: 1.0 mm, genitalia 0.1 mm.

Abbreviations: A, terminal apophysis; C, conductor; E, embolus; M, median apophysis.

Petrunkevitch, AMNH); Selva del Ocoto, 32 km NW Ocozocoautla, 27 Aug. 1973, ♂ (C. Mullinex et al., CAS). BELIZE Mt. Pine Ridge, Feb.–Mar. 1931, ♀ (H. H. Bartlett, MCZ); nr. Río Frío Cave, 5 June 1974, ♂ (C. J. Goodnight, AMNH). GUATEMALA *Los Petén*: Tikal Ruins, 1 July 1980, ♀ (J. Coddington, MCZ); Tikal, July 1975, ♀ (W. Sedgwick, MCZ); 7–12 Aug. 1979, ♀ (C. E. Griswold, T. C. Meikle, CAS). *Izabal*: Los Amates, 1908, ♀♂ (Kellerman, MCZ). *Alta Verapaz*: Lanquin nr. Gruta, 5 Feb. 1980, ♀ (V., B. Roth, AMNH). *Suchitepéquez*: Mocá, June 1947, ♂ (C., P. Vaurie, AMNH); Variedades, 1–4 July 1947, ♀ (C., P. Vaurie, AMNH). HONDURAS *Copán*: Copán, March 1939, ♂ (AMNH). *Atlantida*: Lancetilla, 1929, ♀ (A. M. Chickering, MCZ). NICARAGUA 50 km E Matagalpa, El Coyolar, 800 m, 20 Nov. 1991, ♀♂ (J. Maes, JM); Musawas, Waspuc River, Sep., Oct. 1955, ♀♂ (B. Malkin, AMNH). *Granada*: Volcán Mombacho, 700–800 m, 15 July 1998, ♀ (J. M. Maes, JM). COSTA RICA *Limón*: 20 km N Siquirres, 100 m, July 1980, ♀ (W. Eberhard. MCZ); Hamburg Farm, ♀ (C. R. Dodge, MCZ); Finca La Laja, 190 m, ♀♂ (K. A. Arnold, MCZ). *Heredia*: Puerto Viejo, La Selva, many records (CAS, MCZ, USNM). *Guanacaste*: Orosi, ♀♂ (Picado, MCZ). *Cartago*: Turrialba, many records (AMNH, CUC); Finca Sinfonia, 9°50′N, 83°05′W, 26 Jan. 1976, ♀ (Roth, Schroepfer, AMNH). *San José*: Bajo La Hondura (Braulio Carrillo Natl. Park), 1,400–1,600 m, 26 July 1983 (W. Eberhard, MCZ); Río Hondura, 10°N, 84°W, 1,200 m, 30 Mar. 1991, ♂ (W. Eberhard, MCZ); nr. Villa Colón, 800 m, Nov. 1990, (W. Eberhard, MCZ); San José, ♂ (E. Schmidt). *Puntarenas*: nr. Quepas Manuel-Antonio, 9°23′N, 84°09′W, 15–21 Feb. 1976, ♀ (Roth-Schoepfer, AMNH); 24 km S Volcán, 12 July 1970, ♀ (S. Riechert, AMNH); Osa Peninsula, 3.2 km SW Rincon, 21–28 Feb. 1967, ♀ (J. Nelson, MCZ); Corcovado Natl. Park, Sirena, 25 Feb. 1979, ♀ (J. Coddington, MCZ); Santa Elena nr. Monteverde, 20 June 1998, ♂ (K. J. Ribardo, CAS); Quizarra, 6 km E San Isidro, May 1989, ♀ (W. Eberhard, MCZ); San Isidro del General, 600–1,200 m, ♀ (D. Rounds, MCZ); nr. Tocales, Reserva Carara, Aug. 1983, ♀ (W. Eberhard, MCZ); Golfito, 25 Jan. 1995, ♀ (W. Eberhard, MCZ). PANAMA *Chiriquí*: Bugaba, July 1939, Aug. 1940, ♀ (A. M. Chickering, MCZ); 1, 2 Nov. 1985, ♀ (D. Quintero, MIUP); Cerca Cementerio, Bugaba, Río Mulo, 2 Nov. 1985, ♀♂ (D. Quintero, MIUP); La Fortuna, 1,100–1,200 m, 5 Apr. 1984, ♀♂ (W. Eberhard, MCZ); El Volcán, 20 Mar. 1936, ♀♂ (W. J. Gertsch, AMNH). *Veraguas*: Alto Limón (La Yeguado), 11 Aug. 1984, ♀ (D. Quintero, MIUP); San Martín, Santiago, 21 July 1983, ♀ (M. E. Mendoz, MIUP). *Colón*: Colón, July 1979, ♀ (Broadhead et al., USNM). *Panamá*: El Valle, several records, ♀♂ (AMNH, MCZ); Arraiján, ♀♂ (A. M. Chickering, MCZ); Canal area, very common (MCZ, USNM); Cermeño, Jan.–Feb. 1940, ♂ (Zetek, MCZ); Panama City, July 1979, ♀♂ (E. Broadhead et al., USNM). *Darién*: Villa Darién, 12–18 Feb. 1984, ♂ (M. N. García, MIUP).

TRINIDAD nr. Port of Spain, 1913, ♀♂ (R. Thaxter, MCZ); 9 Feb. 1926, ♀♂ (W. S. Brooks, MCZ); Sangre Grande, 1913, ♀♂ (R. Thaxter, MCZ); Cumuto, Feb. 1926, ♀ (W. S. Brooks, MCZ). *St. Andrew Co.*: Valencia Ward at Oropuche River, 17 Aug. 1986, ♂ (G. B. Edwards, FSCA).

Mangora itza new species
Figures 48–56; Map 1F

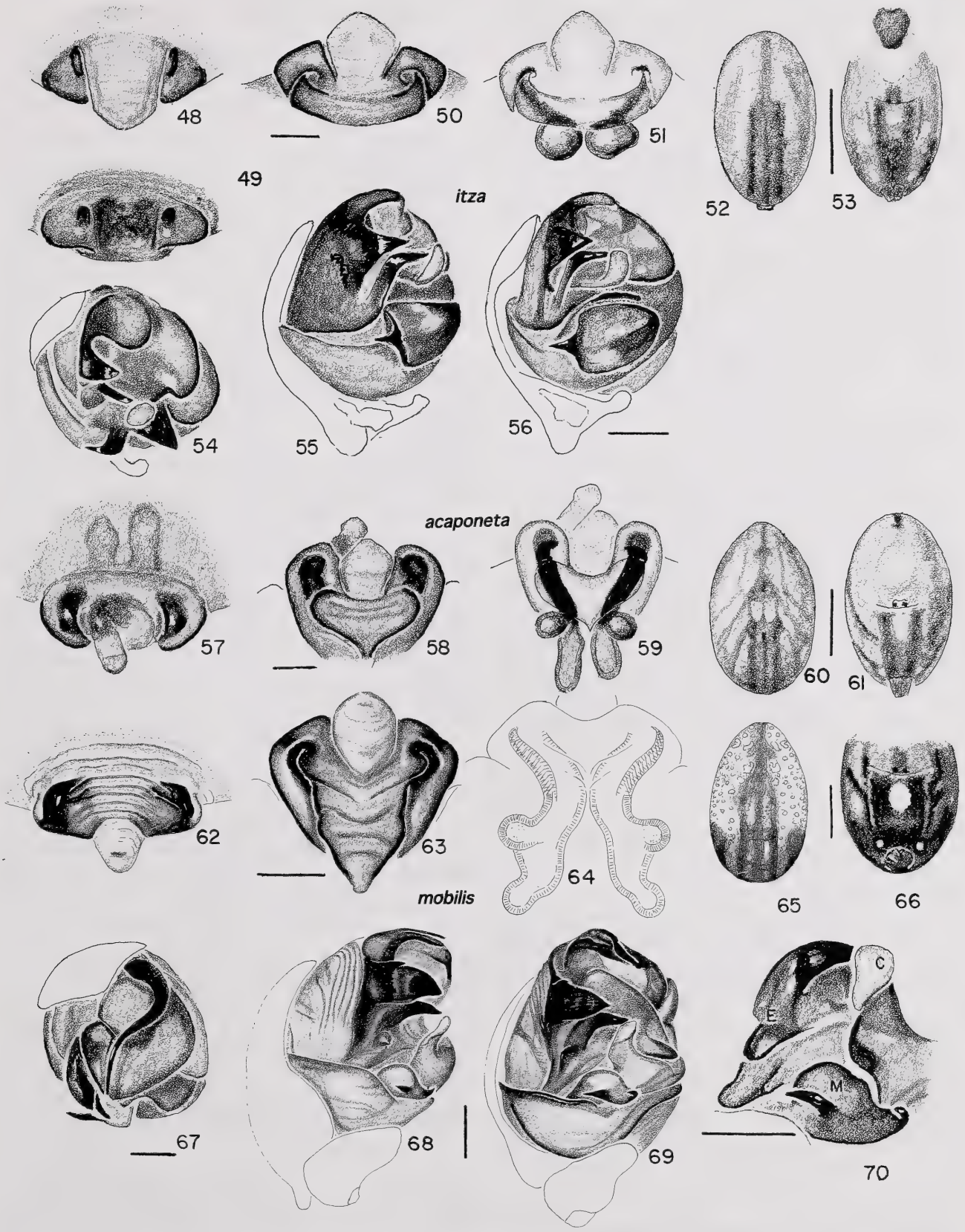
Holotype. Female holotype from Chichen Itza, Yucatan, Mexico, 12 Sep. 1964 (J. C. Pallister), in AMNH. The name is a noun in apposition after the type locality.

Description. Female holotype. Carapace yellowish, with a narrow, median longitudinal gray line. Labium, endites, sternum, legs yellowish; sternum grayish along borders. Abdomen with median, longitudinal dark band that is narrower anteriorly, containing posteriorly three darker bands, sides with scattered white spots (Fig. 52); venter light yellowish, with three white patches and two indistinct darker, longitudinal bands. A pair of white patches on sides (Fig. 53). Posterior eye row procurved. Ocular trapezoid longer than wide, rectangular. Posterior median eyes 1.2 diameters of anterior medians; anterior lateral eyes 1.0 diameter, posterior 0.8. Anterior median eyes their diameter apart, 1.2 from laterals. Posterior median eyes 0.7 diameter apart, 1.2 from laterals. Height of clypeus equals 0.8 diameter of anterior median eyes. Total length 3.5 mm. Carapace 1.7 mm long, 1.3 wide in thoracic region, 0.7 wide behind lateral eyes, 0.7 high. First femur 1.7 mm, patella and tibia 2.1, metatarsus 1.7, tarsus 0.8. Sec-

→

Figures 48–56. *Mangora itza* new species. 48–53, female. 48–51, epigynum. 48, ventral. 49, ventral, scape torn. 50, posterior. 51, posterior, cleared. 52, abdomen, dorsal. 53, abdomen, ventral. 54–56, male, left palpus. 54, apical. 55, mesal. 56. ventral.

Figures 57–61. *Mangora acaponeta* new species, female. 57–59, epigynum. 57, ventral. 58, posterior. 59, posterior, cleared. 60, abdomen, dorsal. 61, abdomen, ventral.



Figures 62–70. *Mangora mobilis* (O. P.-Cambridge). 62–66, female. 62–64, epigynum. 62, ventral. 63, posterior. 64, posterior, cleared. 65, abdomen, dorsal. 66, abdomen, ventral. 67–70, male, palpus. 67, apical. 68, mesal. 69, ventral. 70, median apophysis, conductor and embolus.

Scale lines: 1.0 mm, genitalia 0.1 mm.

ond patella and tibia 1.8 mm, third 1.2. Fourth femur 2.0 mm, patella and tibia 1.8, metatarsus 1.8, tarsus 0.7.

Male paratype. Coloration similar to that of female. Posterior eye row straight. Ocular trapezoid longer than wide, widest anteriorly. Posterior median eyes 0.8 diameter of anterior medians; lateral eyes 0.5 diameter. Anterior median eyes 0.7 diameter apart, 0.7 from laterals. Posterior median eyes 0.3 diameter apart, 1.0 from laterals. Height of clypeus equals 1.0 diameter of anterior median eyes. Total length 2.1 mm. Carapace 1.2 mm long, 0.8 wide in thoracic region, 0.3 wide behind lateral eyes, 0.4 high. First femur 1.4 mm, patella and tibia 1.5, metatarsus 1.3, tarsus 0.6. Second patella and tibia 1.3 mm, third 0.8, fourth patella and tibia 1.8.

Variation. Total length of females 3.5–3.7 mm, males 2.1–2.2 mm. The specimen from Uxmal is darker with a black sternum and black spots on legs. The epigynum is variable: the scape varies in width; in ventral view the lateral sclerites vary in amount of sclerotization; and in posterior view the transverse sclerite varies in sclerotization. One specimen had the scape torn off the epigynum (Fig. 49). The palpus of the male has a large concave median apophysis (4 h in Figs. 55, 56). The illustrations are a composite from various specimens.

Diagnosis. The epigynum of *M. itza* has a wide scape flanked by sclerotized lobes (Fig. 48), and is distinguished from other species by the wide transverse posterior band (Fig. 50).

The male is separated from others by the large concave median apophysis in the palpus with a spine pointing toward the cymbium (4 h in Figs. 55, 56).

Distribution. Yucatan Peninsula.

Paratypes. MEXICO *Campeche*: Campeche, 27, 28 Oct. 1946, 1♀, 1♂ (H. Wagner, AMNH). *Yucatan*: Chichen Itza, 16 July 1952, 1♀ (J. C. Pallister, AMNH); Uxmal, July 1981, 1♀ (C. Gold, CAS); Valladolid, 13 Sep. 1952, 1♂ (J., D. Pallister, AMNH).

Mangora acaponeta new species
Figures 57–61; Map 1F

Holotype. Female holotype from 12.8 km NW Acaponeta, Nayarit, Mexico, 25 Nov. 1948 (H. B. Leech) in CAS.

Description. Female holotype. Carapace light orange, with a median gray line and gray patch on each side of thoracic region. Chelicerae with gray patch. Labium, endites gray. Sternum gray anteriorly and on sides. Legs with fine black rings and black spots at origin of macrosetae. Abdomen dorsum orange-white, with posterior longitudinal bands (Fig. 60); venter with a white patch surrounded by black behind epigynum, lateral diagonal bands, and areas with white pigment spots (Fig. 61). Posterior eye row straight. Ocular trapezoid longer than wide, rectangular. Posterior median eyes 1.0 diameter of anterior medians; lateral eyes 0.8 diameter. Anterior median eyes 0.8 diameter apart, 1.0 from laterals. Posterior median eyes 0.8 diameter apart, 1.2 from laterals. Total length 3.8 mm. Carapace 1.3 mm long, 1.1 wide, 0.6 wide behind lateral eyes, 0.7 high. First femur 1.8 mm, patella and tibia 1.8, metatarsus 1.6, tarsus 0.7. Second patella and tibia 1.7 mm, third 1.1, fourth femur 1.8.

The male is not known.

Diagnosis. The epigynum of *M. acaponeta* is distinguished from that of other species by the lateral plates which in ventral view have a median, dark mark and in posterior view a heart-shaped median plate, pointed behind (Fig. 58).

Distribution. Nayarit (Map 1F).

Specimens Examined. No other specimens have been found.

Mangora mobilis (O. P.-Cambridge)
Figures 62–70; Map 1G

Epeira mobilis O. P.-Cambridge, 1889: 30, pl. 6, fig. 1, ♀. Female specimens from Ciudad in Durango [Mexico] and Motagua Valley, Chicoyoto [? Chiquito], Guatemala in the BMNH, examined, probably not syntypes. Keyserling, 1892: 240, pl. 12, fig. 179, ♀.

Mangora mobilis:—F. O. P.-Cambridge, 1904: 479,

pl. 45, figs. 16, 17, ♀♂. Additional locality from Teapa in Tabasco, Mexico. Platnick, 2004.

Note. The syntypes are lost. The specimen surviving and labeled *mobilis* is the one from Teapa, examined by F. O. P.-Cambridge.

Description. Female from Jalisco. Prosoma light orange, with a gray longitudinal line through middle of carapace. Dorsum of abdomen with three gray lines posteriorly, and posterior black laterally; white pigment spots in light areas (Fig. 65). Venter with patch of white pigment spots behind epigynum on black venter (Fig. 66). Posterior eye row straight. Median eye trapezoid square. Posterior median eyes 1.0 diameter of anterior medians; lateral eyes 0.8 diameter. Anterior median eyes 0.8 diameter apart, 1.0 from laterals. Posterior median eyes 0.8 diameter apart, 1.5 from laterals. Height of clypeus equals 0.8 diameter of anterior median eye. Total length 4.2 mm. Carapace 1.7 mm long, 1.4 wide, 0.7 wide behind eyes, 0.8 high. First femur 1.9 mm, patella and tibia 2.3, metatarsus 1.8, tarsus 0.8. Second patella and tibia 2.2 mm, third 1.2, fourth 2.2.

Male from Jalisco lighter than female, abdomen with two dorsal bands of white pigment spots; venter without marks. Posterior eye row slightly recurved. Median eye trapezoid wider anteriorly than long. Posterior median eyes 0.8 diameter of anterior medians; lateral eyes 0.6 diameter. Anterior median eyes 0.6 diameter apart, 0.6 from laterals. Posterior median eyes 0.5 diameter apart, 1.3 from laterals. Total length 2.8 mm. Carapace 1.5 mm long, 1.3 wide in thoracic region, 0.4 wide behind lateral eyes, 0.7 high. First femur 1.8 mm, patella and tibia 2.0, metatarsus 1.6, tarsus 0.9. Second patella and tibia 1.6 mm, third 0.9, fourth 1.5.

Variation. Total length of females 3.2–4.3 mm, males 2.4–2.8 mm. Rarely the sternum is black and the legs have small, black patches at the insertion of macrosetae. The illustrations (Figs. 67–70) were from a male from Teapa, Tabasco.

Diagnosis. The epigynum of *M. mobilis,* in posterior view, has the median plate longer than wide (Fig. 63), unlike the related species *M. acaponeta, M. distincta,* and *M. amchickeringi,* which have the plate wider than long (Figs. 58, 72, 81). It differs from *M. fascialata,* which has a similar epigynum, by lacking the ventral black lines on the venter of the femora as seen in *M. fascialata* (Fig. 100).

The palpus of the male has a short sclerotized, triangular median apophysis, wider on one end than the other (Fig. 70).

Natural History. Specimens came from tropical, deciduous forest in Jalisco; pine forest in Chiapas.

Distribution. Mexico to western Honduras (Map 1G).

Specimens Examined. MEXICO *Tamaulipas*: 3.2 km E Nuevo Morelos, 2 Dec. 1939, 1♀ (L. I. Davis, AMNH); Naciemente del Río Frío, nr. Gomez Farias, 23°1′N, 99°1′W, 6, 7 June 1983, 1♀ (W. Maddison, MCZ); 9.6 km E Villa Juarez, 7 July 1941, 7♀ (L. I. Davis, AMNH); ridge betw. Antiguo Morelos and Nuevo Morelos, 18 Nov. 1948, 1♀ (H. B. Leech, CAS). *Coahuila*: 19.8 km S Saltillo, 4 July 1985, 1♀ (J. Woolley et al., AD). *Sonora*: 13 km W Alamos, 23 Aug. 1965, 1♂ (W. J. Gertsch et al., AMNH). *San Luis Potosí*: Ciudad del Maiz, 760 m, 28 July 1953, 1♂ (C. J. Goodnight, AMNH); El Salto, 21–23 June 1955, 1♀ (C., P. Vaurie, AMNH); Huichichuyan, 19 May 1952, 1♀, 1♂ (W. J. Gertsch et al., AMNH); Limonoito, 16 Aug. 1964, 1♀, 1♂ (J. W. Ivie, AMNH); Picolo, 21 May 1952, 1♀, 1♂ (M. Cazier et al., AMNH); Pujal, 19 May 1952, 1♀ (W. J. Gertsch, AMNH); 13 km W San Joaquin, 19 Apr. 1963, 1♀, 1♂ (W. J. Gertsch, W. Ivie, AMNH); Tamazunchale, 8 July 1944, 2♀ (L. I. Davis, AMNH); 23 Nov. 1946, (E. S. Ross, CAS); 20 May 1952, many ♀♂ (W. J. Gertsch et al., AMNH); 20 July 1956, 1♀, 2♂ (W. Gertsch, V. Roth, AMNH); 13 km NNW Tamazunchale, 19 Apr. 1963, 1♂ (W. J. Gertsch, W. Ivie, AMNH); 1.6 km SW Tamazunchale, 29 July 1966, 1♀ (J., W. Ivie, AMNH); Valles, 1961, 1♂ (L. Staude, AMNH); 19 July 1956, 1♀, 3♂ (W. J. Gertsch, V. Roth, AMNH); 15 Aug. 1964, 1♂ (J., W. Ivie, AMNH); Valles El Bañito, 27 June, 1940, 1♀ (H. Hoogstraal, MCZ); 8 km N Valles, 17 Apr. 1938, 1♀ (L. I. Davis, AMNH); 32 km S Valles, 14 Apr. 1946, 1♂ (A. M., L. I. Davis, AMNH); Volcán San Martín, nr. San Andrés, 1,520 m, 14 July 1953, 1♀ (C. J. Goodnight, AMNH). *Durango*: 56 km N Villa Juarez, 17 Apr. 1938, 1♀ (L. I. Davis, AMNH); 1 km S Villa Juarez, 17 Apr. 1938, 2 ♀ (A. M., L. I. Davis, AMNH). *Sinaloa*: Mazatlán, 6 Sep. 1956, 1♂ (A. F. Archer, AMNH); 3.2 km S Elota, 23°55′N, 106°48′W,

11 Sep. 1966, 1♂ (J., W. Ivie, AMNH). *Nayarit*: La Libertad, 6 Aug. 1947, 1♀, 1♂ (J. Goodnight, B. Malkin, AMNH); San Blas, Manbauchen Beach, 9 Sep. 1966, 1♂ (J., W. Ivie, AMNH); 16 km E San Blas, 12 Aug. 1954, 1♀ (R. E. Ryckman et al., AMNH). *Jalisco*: El Limón, 720 m, 19°47′N, 104°03′W, 6 Dec. 1996, 1♀ (Alvarez, Castello, MCZ); 2 Aug. 1997, 1♂; 31 Aug. 1997, 3♀ (F. Alvarez, MCZ); Esta. Biol. Chamela, 100 m., Sep. 1988, 1♀ (W. Eberhard 3515, MCZ); Sep. 1988, 1♀ (W. Eberhard SAE-12B, MCZ); Sep. 1989, 1♂; Sep. 1990, 1♀, 3♂ (W. Eberhard, MCZ); Chamela Station, Aug. 1992, 1♂ (W. Eberhard, MCZ); Puerto Vallarta, Sep. 1957, 1♀ (J. A. Comstock, CUC); hillside above Plan de Barrances, 21°01′N, 104°05′W, 8 Sep. 1966, 2♂ (J., W. Ivie, AMNH). *Colima*: Potrero Grande, 15 Jan. 1943, 1♀ (F. Bonet, AMNH); Orilla Río America, Tecoman, 18 Jan. 1943, 1♀ (F. Bonet, AMNH); Tecolapa, 31 July 1954, 2♀, 1♂ (W. J. Gertsch, AMNH). *Veracruz*: Acayucan, 25 Oct. 1957, 1♀ (R. R. Dreisbach, MCZ); 6.4 km NE Acayucan, 27 Apr. 1963, 1♂ (W. J. Gertsch, W. Ivie, AMNH); Alamo, 17 Oct. 1947, 1♀, 1♂ (H. Wagner, AMNH); Catemaco, Playa Azul, 9 Aug. 1966, many ♀♂ (J., W. Ivie, AMNH); Fortín, 25 July 1956, many ♀♂ (V. Roth, W. J. Gertsch, AMNH); 5 Aug. 1966, 3♀ (J. W. Ivie, AMNH); Córdoba, 11–13 May 1946, many ♀♂ (J. C., D. L. Pallister, AMNH); 21 Sep. 1984, 1♀, 1♂ (C. W. Agnew et al., AD); 4.8 km NE Huatusco, 22 July 1985, 1♀ (J. Woolley et al., AD); La Buena Ventura, July 1909, many ♀♂ (A. Petrunkevitch, AMNH); Lake Catemaco, 330 m, 26 July 1955, 1♀ (C., P. Vaurie, AMNH); Los Tuxtlas, 15 km N Catemaco, Aug. 1986, 1♀ (W. Eberhard, MCZ); July 1990, 1♀ (B. Traw, MCZ); Mantla, 1, 2 July 1946, many ♀♂ (H. Wagner, AMNH); Martinez de la Torre, 4, 5 July 1946, 2♀, 2♂ (H. Wagner, AMNH); Papantla, 12 Oct. 1947, many ♀♂ (H. Wagner, AMNH); 24 Aug. 1946, 3♀ (J. Goodnight et al., AMNH); Plan del Río, 26 July 1956, 1♀ (V. Roth, W. J. Gertsch, AMNH); Potrero, 24 June 1936, 1♀ (L. I. Davis, AMNH); San Rafael [Carretore, Mantla Martinez], 3 July 1946, 2♀, 1♂ (H. Wagner, AMNH); 4 km N Sontecomapan, 21 Aug. 1967, 1♀ (R. E. Leech, CNC); Tecolutla, 13 Oct. 1947, many ♀♂ (H. Wagner, AMNH); Tierra Colorado, 26 July 1956, 1♂ (W. J. Gertsch, V. Roth, AMNH); Tlapacoyan, 300 m, 7, 8 July, 1946, many ♀♂ (H. Wagner, AMNH). *Michoacan*: 78 km SE Aquila, 13 July 1984, 1♂ (J. Woolley, AD); 16 km S Uruapan, 6, 7 July 1985, 2♀ (J. Woolley et al., AD). *Puebla*: Acatlan, 24–27 Sep. 1946, 1♀ (H. Wagner, AMNH). *Guerrero*: Arcelio, 400 m, 2 Nov. 1947, 2♀ (H. Wagner, AMNH); Iguala, 730 m, 27 Oct. 1947, 1♂ (H. Wagner, AMNH); 1.6 km NE La Laguna, 17 July 1984, 2♀, 1♂ (J. Woolley, AD). *Oaxaca*: Huajuapan, 27 Sep.–1 Oct. 1946, 1♀ (H. Wagner, AMNH); Jalapa, 28 Aug. 1947, 3♀, 1♂ (H. Wagner, AMNH); San Felipe, nr. Oaxaca City, 1,700 m, 6 Oct. 1946, 3♀ (H. Wagner, AMNH); Papaloapan, 24, 25 July 1946, 1♀ (H. Wagner, AMNH); Paso Real, Río Tonto, 28, 29 July 1946, many ♀♂ (H. Wagner, AMNH); Playa Hati, Río Tonto, 27 July 1946, many ♀♂ (H. Wagner, AMNH); Puerto Escondido, 15 July 1985, 1♂ (J. Woolley et al., AD); 7 km NE San Pedro Mixtepec, 16 July 1985, 1♂ (J. Woolley et al., AD); Soyaltepec, 1, 2 Aug. 1946, many ♀♂ (H. Wagner, AMNH); Tehuantepec, 26 Aug. 1947, many ♀♂ (H. Wagner, AMNH); Tuxpan, 15 Oct. 1947, many ♀♂ (H. Wagner, AMNH); Tuxtila, 23 July 1946, 3♀, 3♂ (H. Wagner, AMNH); 22 km W Zanatepec, 28 Aug. 1967, ♀ (R. E. Leech, REL). *Tabasco*: Villahermosa (La Venta), 18°00′N, 92°53′W, 13 Aug. 1966, 1♀ (J. W. Ivie, AMNH). *Campeche*: Campeche, 27, 28 Oct. 1946, 2♀ (H. Wagner, AMNH); San José, Dec. 1946, 2♀, 1♂ (H. Wagner, AMNH). *Yucatan*: Piste, 4–8 June 1959, 1♀ (C., P. Vaurie, AMNH); 4 km N of Xocenpich, 12 km N of Piste, ca. 20°47′N, 88°34′W, 20 July 1983, 1♀, 1♂ (W. Maddison, MCZ); Uxmal, 18 Aug. 1949, 1♂ (C. J. Goodnight, AMNH). *Chiapas*: Arriaga, low coast, 1, 2 Sep. 1947, 3♀, 4♂ (H. Wagner, AMNH); 24 km NW Arriaga, 27 Aug. 1966, 5♀ (J., W. Ivie, AMNH); Chiapa, 6 Sep. 1947, 1♀, 3♂ (H. Wagner, AMNH); Cintalapa, 17 Sep. 1947, 3♀, 1♂ (H. Wagner, AMNH); Escuintla, 1♀, 3♂ (N. Banks, MCZ); 3♂ (Crawford, MCZ); Las Cruces, 15–18 Sep. 1947, 2♀ (H. Wagner, AMNH); Puerto Madero [Puerto de San Benito], 2 Aug. 1950, 2♂ (C., M. Goodnight, AMNH); Ocosingo, 24, 25 June 1950, 4♀ (C., M. Goodnight et al., AMNH); Río de Las Flores, 15 Sep. 1947, 3♂ (H. Wagner, AMNH); Río San Gregorio, km 1,327, betw. Comitan and Ocotal, 18 July 1950, 1♂ (C., M. Goodnight, AMNH); nr. Simojovel, 4 Aug. 1964, 1♀ (J. Shatterly, MCZ); Tonala, Aug. 1909, 1♀, 1♂ (A. Petrunkevitch, AMNH). GUATEMALA *Baja Verapaz*: San Jerónimo, 24, 26 July 1947, 1♀ (C., P. Vaurie, AMNH). *Chiquimula*: Chiquimula, 375 m, 21–23 July 1947, 1♀ (C., P. Vaurie, AMNH). *Suchitepequez*: Variedades, 1–4 July 1947, 1♀ (C., P. Vaurie, AMNH). EL SALVADOR Santa Tecla [13°41′N, 89°17′W], 15 Oct. 1949, 1♀ (J. Boursot, AMNH). HONDURAS *Copán*: Copán, El Cedro, March 1939, 1♂ (AMNH); Copán ruins, 7 March 1939, 1♀ (R. V. Chamberlin, AMNH).

Mangora distincta Chickering
Figures 71–79; Map 1H

Mangora distincta Chickering, 1963: 6, figs. 8–11, ♂. Male holotype from Escuela Agricultura Panamer-

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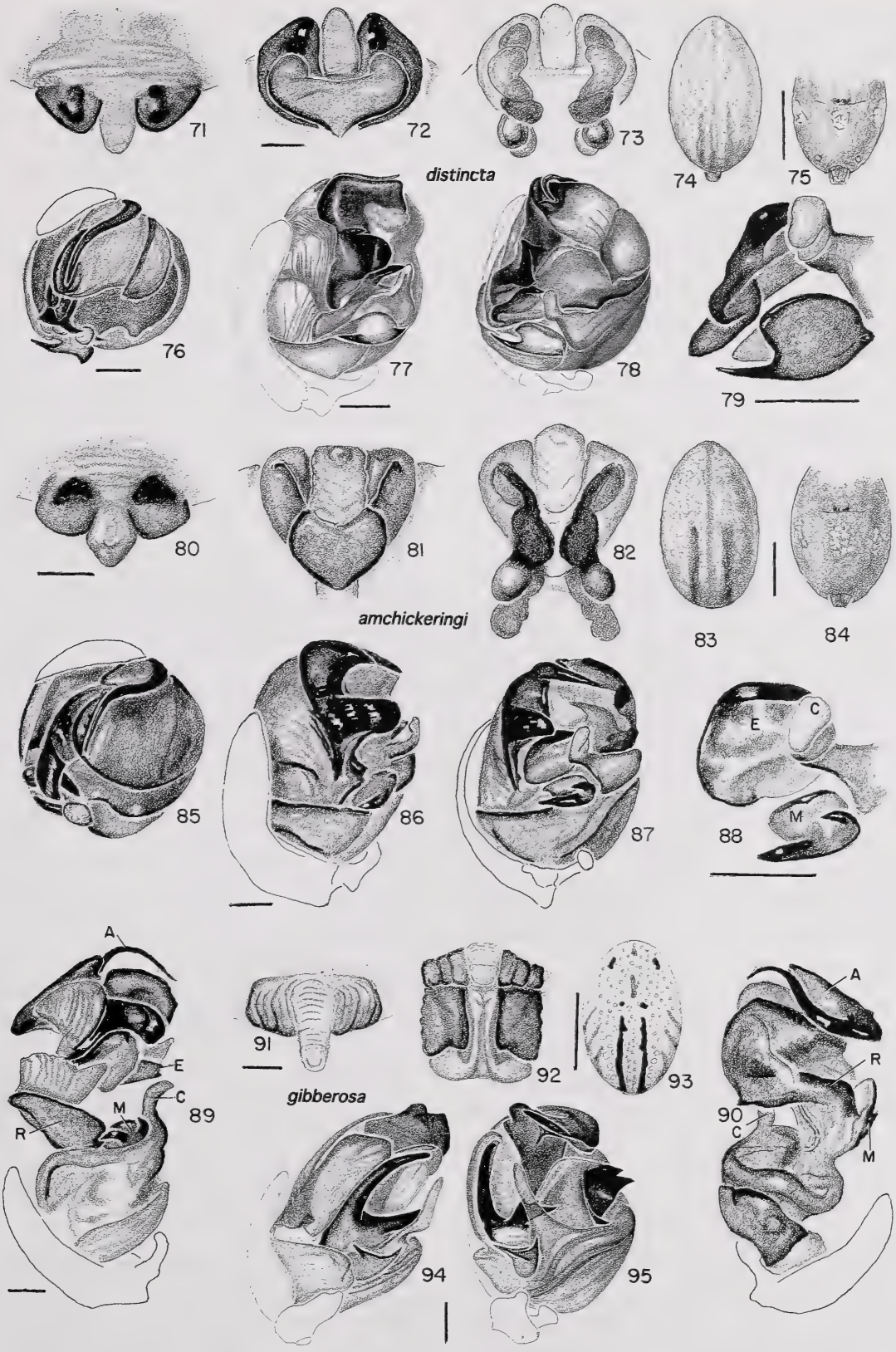
Figures 71–79, *Mangora distincta* Chickering. 71–75, female. 71–73, epigynum. 71, ventral. 72, posterior. 73, posterior, cleared. 74, abdomen, dorsal. 75, abdomen, ventral. 76–79, male, left palpus. 76, apical. 77, mesal. 78, ventral. 79, median apophysis, conductor and embolus.



Figures 80–90, *Mangora amchickeringi* new species. 80–84, female. 80–82, epigynum. 80, ventral. 81, posterior. 82, posterior, cleared. 83, abdomen, dorsal. 84, abdomen, ventral. 85–90, male, palpus. 85, apical. 86, mesal. 87, ventral. 88, median apophysis, conductor and embolus. 89, 90, left palpus, expanded.

Figures 91–95. *Mangora gibberosa* (Hentz). 91–93, female. 91, 92, epigynum. 91, ventral. 92, posterior. 93, abdomen, dorsal. 94, 95, male, palpus. 94, mesal. 95, ventral.

Scale lines: 1.0 mm, genitalia 0.1 mm.

Abbreviations: A, terminal apophysis; C, conductor; E, embolus; M, median apophysis; R, radix.

icana, San Antonio de Oriente, 27 km S [east] of Tegucigalpa, Honduras in MCZ, examined. Platnick, 2004.

Note. Chickering (1954, 1963) did not mention *M. mobilis* in his long description of the very similar *M. distincta* and gives no differential characters. He illustrated the palpus of *M. mobilis* from one side, and that of *M. distincta* from another.

Description. Female from Nicaragua. Prosoma light orange. Abdomen orange-white with white pigment spots and with posterior median three indistinct longitudinal lines (Fig. 74); venter with small area of white pigment spots behind epigynum, and two areas of white pigment spots on each side (Fig. 75). Posterior eye row slightly recurved. Ocular trapezoid longer than wide, about rectangular. Posterior median eyes 1.3 diameters of anterior medians; anterior lateral eyes 0.6, posterior 1.0. Anterior median eyes 1.0 diameter apart, 1.5 from laterals. Posterior median eyes 0.5 diameter apart, 1.2 from laterals. Height of clypeus equals 0.8 diameter of anterior median eyes. Total length 4.2 mm. Carapace 1.7 mm long, 1.4 wide in thoracic region, 0.7 wide behind eyes, 0.7 high. First femur 2.0 mm, patella and tibia 2.2, metatarsus 1.8, tarsus 0.8. Second patella and tibia 1.9 mm, third 1.3. Fourth femur 2.0 mm, patella and tibia 2.0, metatarsus 1.7, tarsus 0.7.

Male holotype. Coloration as in female. Posterior eye row slightly recurved. Ocular trapezoid longer than wide, widest anteriorly. Posterior median eyes 1.0 diameter of anterior medians; laterals 0.7. Anterior median eyes 0.7 diameter apart, 0.7 from laterals. Posterior median eyes 0.4 diameter apart, 1.2 from laterals. Total length 2.4 mm. Carapace 1.2 mm long, 0.9 wide behind eyes, 0.4 wide behind lateral eyes, 0.5 high. First femur 1.4 mm, patella and tibia 1.5, metatarsus 1.3, tarsus 0.6. Second patella and tibia 1.3 mm, third 0.9, fourth 1.3.

Variation. Total length of females 3.2–4.5 mm, males 2.3–2.8 mm. The illustrations were made from females from Nicaragua, and the palpus from the male holotype.

Diagnosis. The epigynum of *M. distincta* is distinguished from epigyna of *M. mobilis* and *M. amchickeringi* by the wide, transverse median posterior plate having two lateral lobes (Fig. 72).

Males differ from these two species by the curved "upper" edge of the median apophysis (Fig. 79).

Natural History. Specimens have been found in dry forests on Volcán Mombacho, in malaise traps; from undergrowth in coffee plantation; in tropical dry forest remnants and organic coffee plantation in Nicaragua.

Distribution. From southeastern Honduras to Costa Rica (Map 1H).

Specimens Examined. NICARAGUA Islas de Solentiname, 30 July 1989, 1♀ (J. Maes, JM); Apanas, 15 July 1989, 1♂ (F. Reinbold, JM); Masaya Las Flores, 1 Aug. 1994, 1♂ (J. M. Maes, JM); 50 km E Metagalpa, El Coyolar, 800 m, 20 Nov. 1991, 3♂ (J. Maes, JM); San Ramon de Tres Ríos, Sep. 1991, 1♀ (J. M. Maes, JM). *Granada*: Volcán Mombacho, Mar.–Aug. 1998, 2♀, 14♂ (J. M. Maes, MCZ). COSTA RICA *Guanacaste*: Bagaces, Palo Verde, 16–22 Jan. 1978, 3♀, 1♂ (W. Eberhard 1316, MCZ); Río Portrero, Bagaces, 7 July 1966, 1♀ (S. Peck, AMNH); ca. Cañas, 100 m, Nov. 1982, 1♀ (W. Eberhard, MCZ); 9.5 km W Cañas, Taboga, 10°19′N, 85°09′W, 1967, 1♀ (J. Nelson, MCZ). *San José*: San José, 1♂ (E. Schmidt, MCZ).

Mangora amchickeringi new species
Figures 80–90; Map 1I

Holotype. Female holotype, 17 male and 39 female paratypes from Madden Dam, Canal Zone, Panama, July 1950 (A. M. Chickering) in MCZ. The species is named after the collector, arachnologist A. M. Chickering.

Mangora mobilis:—Chickering, 1954: 202, figs. 10–14, ♀♂ (misidentification).

Description. Female holotype. Carapace yellow. Abdomen speckled white except midline, with posterior pair of longitudinal black bands (Fig. 83); venter with a patch of white spots behind epigynum and white spots on sides (Fig. 84). Posterior eye row straight. Ocular trapezoid longer than wide, rectangular. Posterior median eyes 1.3 diameters of anterior medians; lateral

eyes 0.8 diameter. Anterior median eyes 0.8 diameter apart, 1.1 from laterals. Posterior median eyes 0.5 diameter apart, 1.1 from laterals. Height of clypeus equals 0.8 diameter of anterior median eyes. Total length 3.9 mm. Carapace 1.7 mm long, 1.4 wide in thoracic region, 0.7 wide behind lateral eyes, 0.7 high. First femur 2.2 mm, patella and tibia 2.3, metatarsus 1.9, tarsus 0.8. Second patella and tibia 2.0 mm, third 1.2. Fourth femur 2.1 mm, patella and tibia 2.2, metatarsus 1.8, tarsus 0.8.

Male paratype. Coloration as in female, except abdomen has a pair of longitudinal, dorsal bands with white pigment spots. Posterior eye row slightly procurved. Ocular trapezoid longer than wide, rectangular. Posterior median eyes 1.2 diameters of anterior medians; lateral eyes 0.6 diameter. Anterior median eyes 0.7 diameter apart, 1.0 from laterals. Posterior median eyes 0.6 diameter apart, 1.3 from laterals. Height of clypeus equal to 0.8 diameter of anterior median eye. Total length 2.6 mm. Carapace 1.3 mm long, 1.1 wide in thoracic region, 0.4 wide behind lateral eyes, 0.5 high. First femur 1.6 mm, patella and tibia 1.8, metatarsus 1.4, tarsus 0.7. Second patella and tibia 1.5 mm, third 0.8, fourth 1.4.

Variation. Total length of females 3.2–4.2 mm, males 2.3–2.8 mm. *Mangora amchickeringi* has less black pigment than *M. mobilis*, but coloration is variable. The female dark, abdominal band is present in most males. The illustrations were made from female holotype and male paratype.

Diagnosis. Ventrally the epigynum of *M. amchickeringi* is like that of *M. mobilis*; however, in posterior view it differs by having a transverse V-shaped, median plate without folds or lobes (Fig. 81), whereas that of *M. mobilis* is longer than wide with many folds (Fig. 63) and the median plate of *M. disticta* has lateral lobes (Fig. 72).

The male differs by having the two teeth of the median apophysis large and directed toward the cymbium, and by the straight "upper" edge of the median apophysis (Fig. 88).

Natural History. Fogging trees in middle savanna in Calabozo, Venezuela, has collected the species.

Distribution. Panama to Venezuela, Trinidad (Map 1I).

Paratypes. PANAMA *Bocas del Toro*: Río Changuinola, Campamente Irie, 13–17 Mar. 1980, 1♀ (R. Ibánez, MCZ). *Cocle*: Cermeño, Feb. 1940, 1♀ (A. M. Chickering, MCZ). *Panamá*: Barro Colorado Isl., several collections (A. M. Chickering, MCZ); Madden Dam, many collections (A. M. Chickering, MCZ); Summit, July 1950, many ♀♂; Aug. 1950, 1♀ (A. M. Chickering, MCZ); Chilibre, July 1950, 1♂ (A. M. Chickering, MCZ); Experimental Gardens, 29 July 1954, 1♀; 12 Aug. 1954, 1♀ (A. M. Chickering, MCZ).

WEST INDIES. TRINIDAD St. Augustine University, April 1964, 1♀, 3♂ (A. M. Chickering, MCZ); Port of Spain, 1913, 1♀, 3♂ (R. Thaxter, MCZ); Gasparce, 3 Nov. 1944, 1♀ (R. H. Montgomery, AMNH). *St. George Co.*: Diego Martin Ward, Edith Falls, Trail, 18 Aug. 1986, 1♂ (G. B. Edwards, FSCA); San Rafael Ward, E side of Talparo River, 20 Aug. 1986, 1♂ (G. B. Edwards, FSCA). *St. Andrew Co.*: Valencia Ward, at Oropuche River, 17 Aug. 1986, 1♂ (G. B. Edwards, FSCA).

VENEZUELA *Bolívar*: San Felix, Oct.–Dec. 1947, 1♀ (AMNH). *Guarico*: Estacion Biológica de los Llanos, Calabozo, 280 m, 18 Jan. 1985, 1♀ (J. Palmer, MCZ); Hato Masaquarai, 45 km S of Calabozo, 17 Mar. 1980, 1♀ (K. Rabenold, MCZ). COLOMBIA *Magdalena*: 10 km E Santa Marta, Oct. 1985, 1♀ (H.-G. Müller, SMF).

Mangora gibberosa (Hentz)
Figures 91–96; Map 1J

Epeira gibberosa Hentz, 1847: 477, pl. 31, fig. 20, ♀. Types from Alabama, destroyed.

Mangora gibberosa:—Levi, 1975, figs. 118–130, ♀♂, map 4. Platnick, 2004.

Description. Description is found in Levi (1975).

Diagnosis. Unlike other *Mangora*, except *M. fascialata* (Fig. 100), specimens have the venter of the first and second femora with a black line.

The female differs from *M. fascialata* by having, in posterior view, rectangular lateral plates (Fig. 92).

The male differs, in apical view of the palpus (Fig. 96), by lacking the wide band present in *M. fascialata* (Fig. 101).

Distribution. Southeastern Canada, eastern United States, only one record from Mexico (Map 1J).

Additional record. MEXICO *Tamaulipas*: Nueva Laredo, 22 July 1946, 1♀ (J. C., D. L. Pallister, AMNH).

Mangora fascialata Franganillo
Figures 97–103; Map 2A

Mangora fascialata Franganillo, 1936: 83. Specimens came from Cuba. Levi, 1975: 128, figs. 110–117, ♀♂. Platnick, 2004.

Mangora striatipes Bryant, 1945: 375, figs. 17, 18, ♀♂. Male holotype from Puerto Plata, Dominican Republic, in MCZ, examined. Synonymized by Levi, 1975.

Mangora conspicua Chickering, 1963: 191, pl. 2, figs. 1–7, ♀♂. Female holotype from El Potosí, Nuevo Léon, Mexico, in MCZ, examined. Synonymized by Levi, 1975.

Description. Female from Nuevo León. Carapace whitish with a median dusky line. Legs whitish with a median black line under the first and second femora (Fig. 100); other articles with black patches. Abdomen light with marks as in Figures 99 and 100. Posterior eye row straight. Ocular trapezoid longer than wide, widest anteriorly. Posterior median eyes 0.9 diameter of anterior medians; lateral eyes 0.7 diameter. Anterior median eyes 1.0 diameter apart, 1.0 from laterals. Posterior median eyes 0.8 diameter apart, 1.0 from laterals. Total length 3.6 mm. Carapace 1.4 mm long, 1.0 wide in thoracic region, 0.6 wide behind lateral eyes, 0.7 high. First femur 1.7 mm, patella and tibia 1.5, metatarsus 1.4, tarsus 0.7. Second patella and tibia 1.4 mm, third 0.9, fourth 1.5.

Male from Haiti. Coloration lighter than in female. Posterior eye row straight. Ocular trapezoid longer than wide, widest anteriorly. Posterior median eyes 1.0 diameter of anterior medians; lateral eyes 0.6 diameter. Anterior median eyes 1.0 diameter apart, 1.0 from laterals. Posterior median eyes 0.4 diameter apart, 1.5 from laterals. Total length 2.2 mm. Carapace 1.2 mm long, 1.0 wide in thoracic region, 0.4 wide behind lateral eyes, 0.6 high. First femur 1.2 mm, patella and tibia 1.2, metatarsus 1.0, tarsus 0.5. Second patella and tibia 1.1 mm, third 0.6, fourth 1.1.

Variation. Total length of females 2.8–3.7 mm, males 2.1–2.3 mm.

Diagnosis. Mangora fascialata is the only species known from the West Indies (except Trinidad). As in *M. gibberosa,* it has a distinct black line along the venter of the first and second femora (Fig. 100).

The lightly sclerotized epigynum is distinguished from others by the presence of a scape and distinctly curved, lateral plates surrounding the median plate in posterior view (Fig. 98). The black line on the venter of the femora of *M. fascialata* prevents confusion with the similar *M. mobilis.*

Males have four or five macrosetae on the venter of the second tibia, and are further distinguished by the numerous sclerites in the palpus (Figs. 101–103). In apical view the palpus has a structure that looks like a wide, tucked-in band (Fig. 101).

Natural History. Specimens came from cane and mesquite along river in Texas; on low shrubs and herbs in Bocatoma, Tamaulipas, and in creek bed in Nuevo León.

Distribution. Texas, Mexico to Honduras, Greater Antilles (Map 2A).

Specimens Examined. TEXAS *Comal Co.*: New Braunfels, 7 June 1942, 1♀ (E. S. Ross, CAS). *Brewster Co.*: Big Bend National Park, Boquillas Camp, 24, 25 May 1967 (E. Sabath, MCZ). MEXICO *Ta-*

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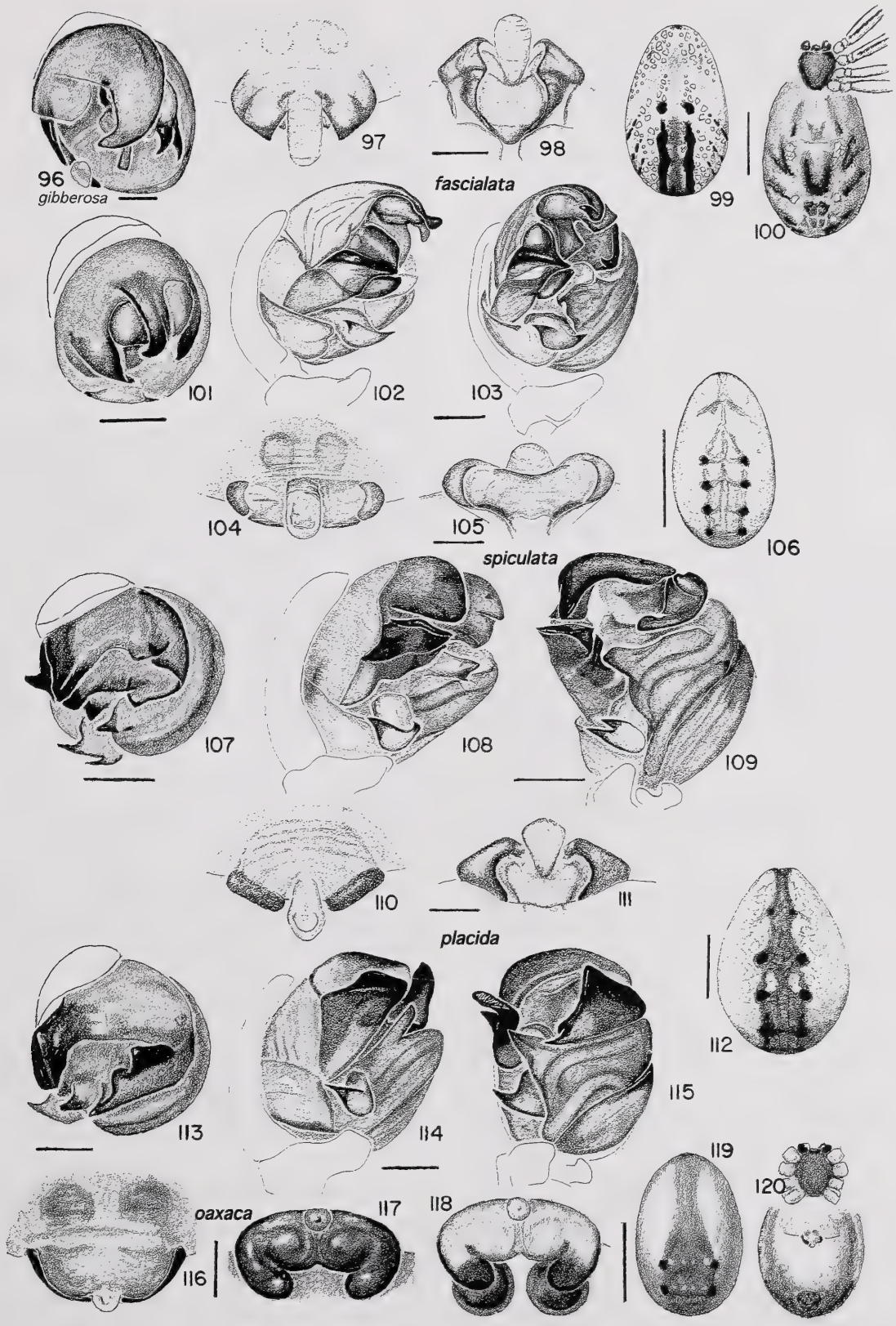
Figure 96. *Mangora gibberosa* (Hentz), male, left palpus, apical.

Figures 97–103. *Mangora fascialata* Franganillo. 97–100, female. 97, 98, epigynum. 97, ventral. 98, posterior. 99, abdomen, dorsal. 100, abdomen, sternum, and proximal parts of left legs, ventral. 101–103, male, palpus. 101, apical. 102, mesal. 103, ventral.

Figures 104–109. *Mangora spiculata* (Hentz). 104–106, female. 104, 105, epigynum. 104, ventral. 105, posterior. 106, abdomen, dorsal. 107–109, male, palpus. 107, apical. 108, mesal. 109, ventral.



Figures 110–115. *Mangora placida* (Hentz). 110–112, female. 110, 111, epigynum. 110, ventral. 111, posterior. 112, abdomen, dorsal. 113–115, male, palpus. 113, apical. 114, mesal. 115, ventral.

Figures 116–120. *Mangora oaxaca* new species, female. 116–120, epigynum. 116, ventral. 117, posterior. 118, posterior, cleared. 119, abdomen, dorsal. 120, abdomen and sternum, ventral.

Scale lines: 1.0 mm, genitalia 0.1 mm.

maulipas: Bocatoma, 26 Feb. 1976, 1♀ (W. B. Peck, CAS); 1.6 km S Antiguo Morelos, 21 July 1954, 1♀ (Chilcott, CNC); Padilla, 17 May 1952, 2♂ (W. J. Gertsch et al., AMNH); NE of Padilla, 24°03′N, 98°03′W, 21 July 1966, 1♂ (J., W. Ivie, AMNH); Victoria, 17 May 1952, 1♂ (W. J. Gertsch et al., AMNH); Villagrán, 19 July 1956, 1♂ (V. Roth, W. Gertsch, AMNH). *Nuevo Léon*: Linares, 3 July 1941, 2♀, 1♂ (L. I. Davis, MCZ); Los Cristales, Aug. 1972, 1♀ (A. F. Archer, AMNH); Sabinas Hidalgo, 13 June 1940, 2♀ (H. Hoogstraal, MCZ); Villa de Santiago, Hacienda Vista Hermosa, 19 June 1940, 1♀, 1♂ (H. Hoogstraal, MCZ); El Potosí, Cerro Potosí, 13 June 1938, 1♀ (Hoogstraal, MCZ); Montemorelos, 23 May 1952, 1♀ (W. J. Gertsch et al., AMNH). *Coahuila*: Saltillo, 23 Aug. 1947, 1♀ (W. J. Gertsch, AMNH); 20 km S Saltillo, 4 July 1985, 1♀ (J. Woolley et al., AD). *Baja California Sur*: 10 km S San Antonio, 31 Dec. 1976, 1♂ (C. Griswold, L. Vincent, CAS). Sierra San Lázaro, 1♀ (N. Banks, MCZ). *San Luis Potosí*: 4 2 km E Ciudad del Maiz, 29 Nov. 1950, 1♀ (A. M. Davis, AMNH); Valles, 45.6 km S Huizache, 4 July 1985, 1♂ (J. Woolley et al., AD); 19 July 1956, 1♀, 1♂ (V. Roth, W. J. Gertsch, AMNH); 11 km S Tamazunchale, 16 Feb. 1961, 1♀ (D., H. Campbell, CAS). *Durango*: Santa María del Oro, 1,700 m, 28 July 1947, 1♀ (W. J. Gertsch, AMNH). *Veracruz*: Fortín, 25 July 1956, 1♀ (V. Roth, W. Gertsch, AMNH); 4 km NE Huatusco, 22 July 1985, 1♀, 2♂ (J. Woolley et al., AD); Plan del Río, 26 July 1956, 1♀ (V. Roth, W. Gertsch, AMNH); Mirador, Zacualpan, 25 Aug. 1933, 1♂ (W. James, AMNH). *Hidalgo*: Apulco, 6 Oct. 1947, 1♀ (H. Wagner, AMNH); Ixmiquilpan, 16–18 Aug. 1947, 2♀, 1♂ (H. Wagner, AMNH); 3 km SW Jacala, 12 Aug. 1972, 1♂ (G. F. Hevel, USNM). *Guerrero*: 37 km N Chilpancingo, 31 July 1956, 1♂ (V. Roth, W. Gertsch, AMNH); 8 km NE Tixtla de Guerreo, 16 July 1984, 1♀ (J. B. Woolley, AD). *Oaxaca*: 13 km NE El Punto, 18 July 1985, 1♀, 1♂ (J. Woolley et al., AD); Huajuapan, 27 Sep.–1 Oct. 1946, 3♂ (H. Wagner, AMNH); Juan Garcia, 16°31′N, 95°47′W, 1 Sep. 1964, 1♀ (J., W. Ivie, AMNH); Oaxaca, 1,550 m, 2 Oct. 1946, 1♀, 2♂ (H. Wagner, AMNH); 22 Aug. 1947, 1♂ (H. Wagner, AMNH); San Felipe, 24 Aug. 1947, 2♀ (H. Wagner, AMNH). *Yucatan*: Dolores Otero, 13 July 1952, 1♀, 1♂ (J., D. Pallister, AMNH). *Chiapas*: Ocosingo, 900 m, 25 June 1950, 3♀, 1♂ (C., M. Goodnight et al., AMNH); Ocozocoautla, 3 Sep. 1947, 1♀ (H. Wagner, AMNH); Tuxtla Gutierrez, 9 Sep. 1947, 1♀, 1♂ (H. Wagner, AMNH). HONDURAS 27 km S Tegucigalpa, San Antonio del Oriente, 17 Nov. 1945, 3♀, 1♂ (A., M. Carr, MCZ).

CUBA *Pinar del Río*: Sierra del Rosario, nr. Institute of Botany research area, May 1976, 1♀ (R. Levins, MCZ). *Oriente*: Santiago, June 1967, 1♂ (P. Alayon, MCZ); Loma "La Farola" Baracoa, June 1967, 1♀ (P. Alayon, MCZ). HAITI Las Cayes, Les Platons, Nov. 1971, 2♀ (T. Moermond, MCZ); Diquini, 2♂ (W. M. Mann, MCZ); hills nr. Port of Prince, 2 Oct. 1934, 6♀ (P. Darlington, MCZ); nr. Kenscoff, 1,300 m, 1 May 1935, 1♀ (Roys, MCZ). DOMINICAN REPUBLIC Puerto Plata, Apr.–May 1941, 2♀ (D. Hurst, MCZ). TRINIDAD Port of Spain, 1913, 1♀ (R. Thaxter, MCZ); St. Augustine, 1 Apr.1964, 1♀ (A. M. Chickering, MCZ).

Mangora spiculata (Hentz)
Figures 104–109; Map 1K

Epeira spiculata Hentz, 1847: 475, pl. 31, fig. 13, ♀. Female holotype destroyed.

Mangora spiculata:—Levi, 1975: 125, figs. 82–89, ♀♂, map 4. Platnick, 2004.

Description. Description is found in Levi (1975).

Diagnosis. The female differs from *M. placida* by having, in ventral view of the epigynum, longitudinal, sclerotized bars at a distance from the scape (Fig. 104).

The median apophysis of the palpus of *M. spiculata* differs from that of *M. placida* by having two spines (6 h in Fig. 108).

Distribution. Eastern United States to southern Texas (Map 1K). No records are known from Mexico, although specimens can be expected there.

Mangora placida (Hentz)
Figures 110–115; Map 2B

Epeira placida Hentz, 1847: 475, pl. 31, fig. 12, ♀. Female holotype from Alabama, destroyed.

Mangora placida:—Levi, 1975: 126, figs. 80, 81, 90–101, ♀♂; map 4. Platnick, 2004.

Description. Description is found in Levi (1975).

Diagnosis. In ventral view of the epigynum, the female differs from *M. spiculata* by having diagonal bars flanking the scape (Fig. 110).

The median apophysis of the palpus of the male has one spine (6 h in Fig. 114), whereas that of *M. spiculata* has two spines (Fig. 108).

Distribution. Southeastern Canada, eastern United States to Nuevo Léon, Mexico (Map 2B).

Additional Record. MEXICO *Nuevo Léon*: Linares, 8 July 1941, 3♀ (L. I. Davis, AMNH).

Mangora oaxaca new species
Figures 116–120; Map 2C

Holotype. Female holotype from Finca Patichuiz, SE of Oaxaca, Mexico, 22 Oct. 1962 (Gardner) in MCZ.

Description. Female holotype. Carapace light orange. Large black circles around secondary eyes. Chelicerae dusky orange. Labium, endites black. Sternum black. Legs light orange, distally darker. Abdomen with median dorsal gray band, blackish posteriorly with four black spots (Fig. 119); venter black posteriorly, sides with a gray band (Fig. 120). Posterior eye row procurved. Ocular trapezoid longer than wide, rectangular. Posterior median eyes 1.2 diameters of anterior medians; lateral eyes 0.8 diameter. Anterior median eyes their diameter apart, 1.0 from laterals. Posterior median eyes 0.8 diameter apart, 1.3 from laterals. Total length 3.0 mm. Carapace 1.3 mm long, 1.0 wide in thoracic region, 0.6 wide behind lateral eyes, 0.7 high. First femur 1.5 mm, patella and tibia 1.8, metatarsus 1.4, tarsus 0.7. Second patella and tibia 1.6 mm, third 1.0, fourth 1.5 mm.

The male is not known.

Diagnosis. The abdomen of *M. oaxaca* (Fig. 119) resembles that of *M. placida* but the epigynum of the former is a semicircle having a dark, sclerotized, posterior, lateral black frame (Fig. 116), and the posterior view is heavily sclerotized with two lateral, dorsal lobes (Fig. 117).

Distribution. Oaxaca (Map 2C).

Specimens Examined. No other specimens have been found.

Mangora nahuatl new species
Figures 121–125; Map 2C

Holotype. Female holotype from Jalapa, Veracruz, Mexico, July 1981 (C. Gold) in CAS. The specific name is a noun in apposition after the Indians inhabiting the area of the type locality.

Description. Female holotype. Carapace yellowish with median eye area and clypeus black. Endites, labium, sternum black. Legs yellowish. Abdomen orange-white, with posterior median black area, and areas with white pigment spots and gray chevron marks (Fig. 124); sides with a black patch; venter with a median gray area (Fig. 125). Posterior eye row straight. Ocular trapezoid square. Posterior median eyes 1.5 diameters of anterior medians; lateral eyes 1.0 diameter. Anterior median eyes 1.3 diameter apart, 1.0 from laterals. Posterior median eyes 0.5 diameter apart, 0.7 from laterals. Total length 2.8 mm. Carapace 1.3 mm long, 0.9 wide in thoracic region, 0.5 wide behind lateral eyes, 0.7 high. First femur 1.3 mm, patella and tibia 1.4, metatarsus 1.1, tarsus 0.5. Second patella and tibia 1.3 mm, third 0.8, fourth 1.3 mm.

The male is not known.

Diagnosis. The dorsal abdominal markings of *M. nahuatl* (Fig. 124) differ from those of *M. passiva* (Fig. 152). Also, in posterior view of the epigynum, the median plate is wider (Fig. 122), with anterolateral lobes, than that of *M. passiva* (Fig. 149).

Distribution. Veracruz, México, Mexico.

Specimen Examined. MEXICO *México:* Tenango de Valle, 2,400 m, 26–29 Aug. 1946, 1♀ (H. Wagner, AMNH).

Mangora volcan new species
Figures 126–130; Map 2D

Holotype. Female holotype and an immature paratype from El Volcán, Chiriquí, Panama, 24 Feb. 1936 (W. J. Gertsch) in AMNH. The name is a noun in apposition after the type locality.

Description. Female holotype. Carapace pale yellow with eye region black. Labium, endites, sternum black. Coxae pale yellowish, distal leg articles gray. Abdomen whitish with a dorsal, posterior black band that fades anteriorly (Fig. 129); sides each with a black patch; venter with a gray area in middle and black around epigynum (Fig. 130). Posterior eye row straight. Ocular trapezoid slightly wider than long, widest anteriorly. Posterior median eyes 1.0 diameter of anterior medians; lateral eyes 0.7 diameter. Anterior median eyes 1.0 diameter apart, 1.0 diameter from laterals.

Posterior median eyes 0.8 diameter apart, 1.0 from laterals. Total length 2.2 mm. Carapace 1.0 mm long, 0.8 wide in thoracic region, 0.4 wide behind lateral eyes, 0.4 high. First femur 1.0 mm, patella and tibia 1.2, metatarsus 1.0, tarsus 0.5. Second patella and tibia 1.1 mm, third 0.6, fourth 1.0.

The male is not known.

Diagnosis. *Mangora volcan* has the scape of the epigynum almost spherical (Fig. 126), and in posterior view, has a wide trapezoid median plate (Fig. 127). In coloration it is unlike any other Central American species (Figs. 129, 130).

Distribution. Chiriquí, Panama (Map 2D).

Specimens Examined. No other specimens have been found.

Mangora fortuna new species
Figures 131–135; Map 2D

Holotype. Female holotype from El Fortuna, 1,100–1,200 m, Chiriquí, Panama, 5 May 1984 (W. Eberhard) in MCZ. The name is a noun in apposition after the name of the type locality.

Description. Female holotype. Prosoma yellowish, darkest in eye region, legs with distal articles dusky. Sternum with a dusky frame, light in center. Dorsum of abdomen with two gray longitudinal bands, most distinct posteriorly (Fig. 134); venter with a V-shaped gray patch anterior to spinnerets and a dusky mark covering epigynum and on each side of the structure (Fig. 135). Posterior eye row slightly procurved. Ocular trapezoid longer than wide, rectangular. Posterior median eyes 1.0 diameter of anterior medians; lateral eyes 0.8 diameter. Anterior median eyes 1.0 diameter apart, 0.4 from laterals. Posterior median eyes 0.8 diameter apart, 0.8 from laterals. Height of clypeus equals 0.8 diameter of anterior median eyes. Sternum bulging. Total length 2.4 mm. Carapace 1.2 mm long, 0.8 wide in thoracic region, 0.4 wide behind lateral eyes, 0.6 high. First femur 1.2 mm, patella and tibia 1.3, metatarsus 1.1, tarsus 0.6. Second patella and tibia 1.2 mm, third 0.7, fourth 1.2.

The male is not known.

Variation. Total length of females 2.3–2.4 mm. Females may be lighter colored than illustrated (Fig. 134), and the ventral coloration is variable. The illustrations were made from the holotype.

Diagnosis. The epigynum of *M. fortuna* is lightly sclerotized, small, and difficult to study in ventral view (Fig. 131); the oval scape is indistinct unless viewed laterally. The posterior view is more distinct and shows a wide median plate (Fig. 132) more curved than that of *M. volcan* (Fig. 127).

Distribution. Costa Rica, western Panama (Map 2D).

Paratypes. COSTA RICA *Heredia*: La Selva nr. Puerto Viejo, Feb. 1981, 1♀ (W. Eberhard, MCZ); 26 March 1979, 1♀ (J. Coddington, MCZ); 22 Nov. 1981, 1♀ (J. Coddington, MCZ).

Mangora campeche new species
Figures 136–139; Map 2E

Holotype. Female holotype from Reserva de la Biosfera, Calakmul, km 32, Campeche, Mexico, 20 July 1998 (F. Alvarez) in MCZ. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace, sternum, legs, golden yellow, except for black eye rings and a gray ring at distal ends of tibiae and tarsi. Abdomen yellowish white, with a posterior pair of longitudinal black bands, a pair of black spots, and pairs of white patches (Fig. 139). Venter without marks but sides of spinnerets blackish. Posterior eye row recurved. Ocular trapezoid longer than wide, widest an-

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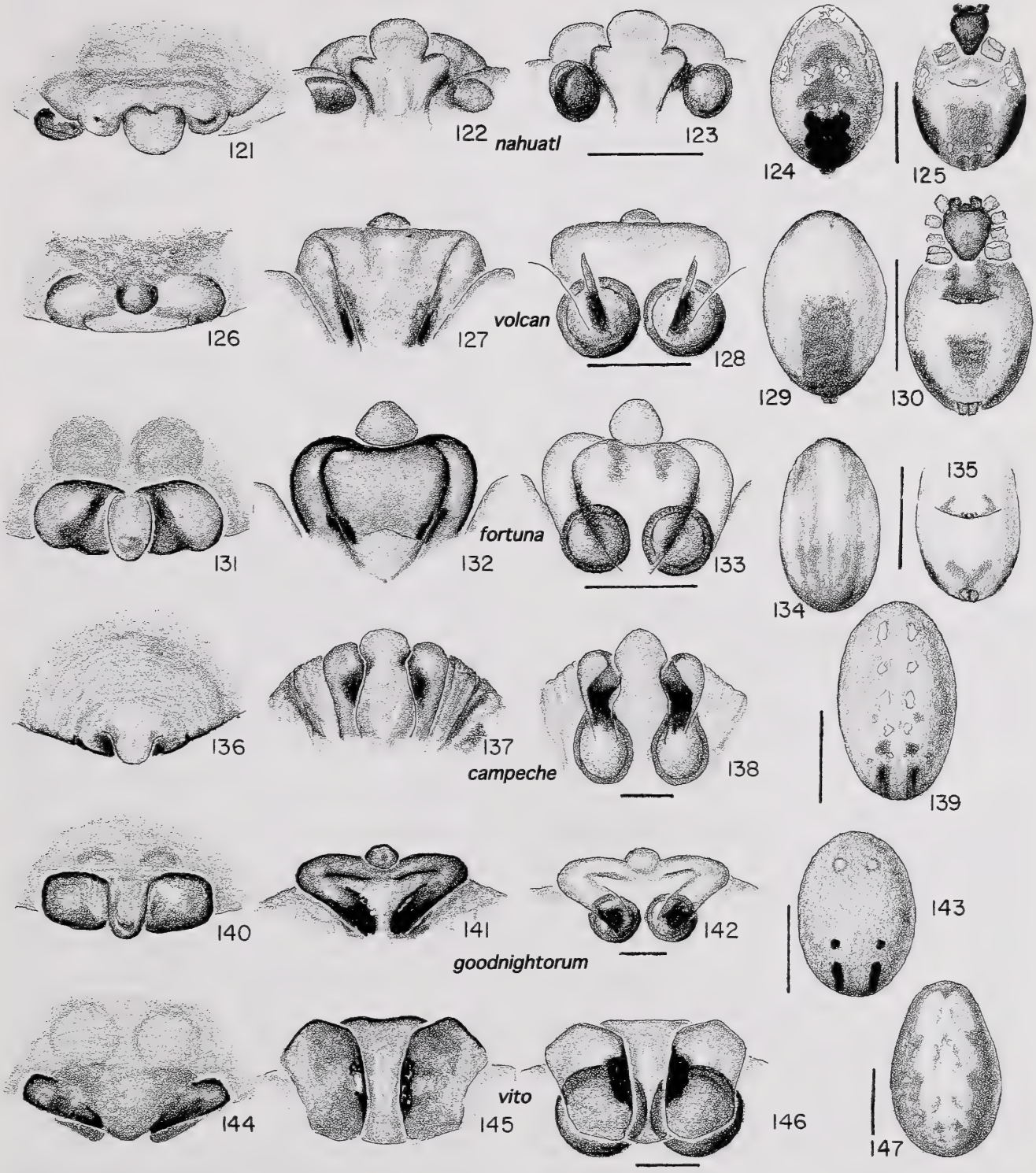
Figures 121–125. *Mangora nahuatl* new species, female. 121–123, epigynum. 121, ventral. 122, posterior. 123, posterior, cleared. 124, abdomen, dorsal. 125, abdomen, ventral.

Figures 126–130. *Mangora volcan* new species, female. 126–128, epigynum. 126, ventral. 127, posterior. 128, posterior, cleared. 129, abdomen, dorsal. 130, abdomen, ventral.



Figures 131–135. *Mangora fortuna* new species, female. 131–133, epigynum. 131, ventral. 132, posterior. 133, posterior, cleared. 134, abdomen, dorsal. 135, abdomen, ventral.

Figures 136–139. *Mangora campeche* new species, female. 136–138, epigynum. 136, ventral. 137, posterior. 138, posterior, cleared. 139, abdomen, dorsal.

Figures 140–143. *Mangora goodnightorum* new species, female. 140–142, epigynum. 140, ventral. 141, posterior. 142, posterior, cleared. 143, abdomen, dorsal.

Figures 144–147. *Mangore vito* new species, female. 144–146, epigynum. 144, ventral. 145, posterior. 146, posterior, cleared. 147, abdomen, dorsal.

Scale lines: 1.0 mm, genitalia 0.1 mm.

teriorly. Posterior median eyes 1.0 diameter of anterior medians; lateral eyes 0.8 diameter. Anterior eyes 1.0 diameter apart, 1.2 from laterals. Posterior median eyes 0.5 diameter apart, 1.5 from laterals. Total length 3.8 mm. Carapace 1.7 mm long, 1.3 wide in thoracic region, 0.7 wide behind lateral eyes, 0.7 high. First femur 1.7 mm, patella and tibia 1.8, metatarsus 1.5, tarsus 0.7. Second patella and tibia 1.7 mm, third 1.2, fourth 1.7.

The male is not known.

Diagnosis. The epigynum of *M. campeche* is lightly sclerotized and distinguished from others, in posterior view, by the narrow, bowling-pin–shaped median plate (Fig. 137).

Distribution. Campeche (Map 2E)

Specimens Examined. No other specimens have been found.

Mangora goodnightorum new species
Figures 140–143; Map 2E

Holotype. Female holotype from Finca Monte Libano [12 mi E El Real], Chiapas, Mexico, "7.5.50" (C., M. Goodnight, J. Stannard), in AMNH.

Description. Female holotype. Prosoma light orange, black between median eyes; distal leg articles gray. Abdomen grayish, light orange with a pair of anterior dorsal white spots and two posterior black bands tipped by a black dot (Fig. 143); venter and spinnerets gray. Posterior eye row straight. Ocular trapezoid longer than wide, widest anteriorly. Posterior median eyes same diameter as anterior medians; lateral eyes 0.8 diameter. Anterior median eyes 1.0 diameter apart, 1.0 from laterals. Posterior median eyes 0.6 diameter apart, 1.3 from laterals. Total length 2.6 mm. Carapace 1.1 mm long, 0.8 wide in thoracic region, 0.4 wide behind lateral eyes, 0.6 high. First femur 1.3 mm, patella and tibia 1.5, metatarsus 0.9, tarsus 0.6. Second patella and tibia 1.3 mm, third 0.8, fourth 1.3.

The male is not known.

Diagnosis. The epigynum of *M. goodnightorum* is sclerotized and is distinguished, in posterior view, from all other Central American *Mangora* by the triangular outline (Fig. 141). Unlike other species, the eye region is slightly projecting above the clypeus.

Distribution. Chiapas (Map 2E).

Specimens Examined. No other specimens have been found.

Mangora vito new species
Figures 144–147; Map 2E

Holotype. Female holotype from San Vito, Las Cruces, 1,300 m, Puntarenas, Costa Rica, Jan. 1987 (W. Eberhard) in MCZ. The specific name is a noun in apposition after the name of the type locality.

Description. Female holotype. Prosoma yellowish. Large black circles around secondary eyes. Legs distally brown. Abdomen white, dorsally with a narrow gray band on each side (Fig. 147), posteriorly wrapping around spinnerets on venter; sides with white pigment spots; venter with gray band anterior of spinnerets. Spinnerets gray. Posterior eye row procurved. Ocular trapezoid longer than wide, widest posteriorly. Posterior median eyes 2.0 diameters of anterior medians; anterior lateral eyes 0.8 diameter, posterior laterals 1.0. Anterior median eyes their diameter apart, 1.0 from laterals. Posterior median eyes 0.5 diameter apart, 0.6 from laterals. Height of clypeus equals 1.5 diameters of anterior median eyes. Total length 3.8 mm. Carapace 1.8 mm long, 1.2 wide in thoracic region, 0.7 wide behind lateral eyes, 0.7 high. First femur 1.5 mm, patella and tibia 1.7, metatarsus 1.3, tarsus 0.6. Second patella and tibia 1.5 mm, third 0.8, fourth 1.6.

The male is not known.

Diagnosis. In ventral view, unlike other species, the epigynum is short, having a median lobe flanked by narrow areas that are lobed laterally, and have a wedge-shaped sclerotization (Fig. 144); in posterior view, the lateral plates overlap the less sclerotized narrow posterior median plate (Fig. 145).

Distribution. Costa Rica (Map 2E).

Specimen Examined. COSTA RICA *San José*: Zurqui, 1600 m, May 1992, 1♀ (W. Eberhard 3632, MCZ) [not mapped].

Mangora passiva (O. P.-Cambridge) Figures 148–156; Map 2F

Epeira passiva O. P.-Cambridge, 1889: 20, pl. 5, fig. 4, ♀. Female syntypes from Cahabón [Alto Verapaz], San Juan [? Alto Verapaz], Chamelco [? Alto Verapaz], Tactic [Alto Verapaz], Chichochoc [?], Laguna de los Coheteros [?], Cobán [Alto Verapaz], all from Guatemala in BMNH, examined.

Epeira rostrata Keyserling, 1893: 230, pl. 11, fig. 171, ♀. Female holotype from Guatemala, in BMNH, examined. Placed by Levi, 1991, in *Mangora*. NEW SYNONYMY.

Mangora passiva:—F. O. P.-Cambridge, 1904: 480, pl. 45, fig. 19, ♀; Levi, 1975: 124, figs. 69–79, ♀♂. Platnick, 2004.

Note. The holotype of *Epeira rostrata* is labeled *Epeira rostralipes* and is shriveled and faded.

Description. Female from Arizona. Carapace, legs yellow-white. Abdomen with a median black band containing large comma-shaped marks formed by white pigment spots and smaller marks (Fig. 152), venter whitish with median white spots behind epigynum, and a pair of white marks anterior of spinnerets (Fig. 153). Posterior eye row recurved. Ocular trapezoid longer than wide, widest anteriorly. Eyes subequal. Anterior median eyes 1.0 diameter apart, 1.5 from laterals. Posterior median eyes 0.9 diameter apart, 2.0 from laterals. Total length 4.7 mm. Carapace 2.0 mm long, 1.7 wide in thoracic region, 0.7 wide behind posterior eye row, 0.8 high. First femur 2.3 mm, patella and tibia 2.5, metatarsus 1.9, tarsus 0.8. Second patella and tibia 2.4 mm, third 1.4, fourth 2.3.

Male from Arizona lighter than female. Eyes subequal. Anterior median eyes 1.0 diameter apart, 1.5 from laterals. Posterior median eyes their diameter apart, 1.5 from laterals. Height of clypeus 0.6 diameter of anterior median eye. Total length 2.7 mm. Carapace 1.3 mm long, 1.2 wide in thoracic region, 0.5 wide behind posterior eyes, 0.7 high. First femur 1.7 mm, patella and tibia 1.9, metatarsus 1.6, tarsus 0.7. Second patella and tibia 1.8 mm, third 0.9, fourth 1.5.

Variation. Total length of females 3.7–4.7 mm.

Diagnosis. The abdomen of *M. passiva* is recognized by the two upside-down, comma-shaped light marks on dark background (Fig. 152). The epigynum is usually lightly sclerotized (Figs. 148, 149); when more heavily sclerotized, it loses wrinkles (Figs. 150, 151). It differs from other lightly sclerotized epigyna by the presence of the short scape and the vase-shaped posterior median plate. *Mangora passive* differs from *M. nahuatl* (Figs. 121–125) by the distinct coloration of the abdomen (Figs. 152, 153) and by being larger in size.

The palpus of the male has a dagger-shaped rod, visible in apical view (Fig. 154), that is heavier than that of *M. sufflava* (Fig. 171).

Natural History. Specimens have been found in short tropical rain forest at Chacanna Ruins.

Distribution. Arizona, New Mexico to Nicaragua (Map 2F; the map includes data from Levi, 1975, map 4).

Specimens Examined. ARIZONA *Cochise Co.*: Rucker Canyon, Chiricahua Mts., 11 July 1973, 1♀ (V. Roth, E. Wilkins, CAS); above Herb Martyr Dam, 11 Aug. 1971, 1♀ (V. Roth, CAS). *Manzanita Co.*: Oak Creek Canyon, 27 July 1950, 3♀, 1♂ (M. A. Cazier, MCZ). MEXICO *Tamaulipas*: 4.5 km NW Gomez Farias, 750 m, 28 Dec. 1971, 2♀ (C. J. Durden, USNM). *Nuévo Léon*: Santa Rosa Canyon, 29 km W Linares, nr. 24°8′N, 99°8′W, 30 June 1983, 1♀ (W. Maddison, MCZ). *San Luis Potosí*: El Pujal, 18–21 July 1939, 1♀ (R. Haag, MCZ). *Jalisco*: Río Rudioso [Río Ruidosa], 2♀ (N. Banks, MCZ). *Veracruz*: 22.5 km S Catemaco on Rt. 180, 23 June 1982, 1♀ (F. Coyle, MCZ); Jalapa, July 1981, 5♀ (C. Gold, CAS); 4.8 km NE Huatusco, 22 July 1985, 2♀ (J. Woolley et al., AD). *Hidalgo*: Jacala, 1,370 m, 30 June–3 July 1939, 1♀ (B. Wathall, AMNH). *Puebla*: Huauchinango, 9 Oct. 1947, many ♀♂ (H. Wagner, AMNH). *Oaxaca*: Llanos de la Flores, 24 km NE Ixtlan de Juárez, 21 July 1985, 1♂ (J. Woolley, et al., AD); base San Filipe Mt., 16, 17 Sep. 1947, 1♂ (B. Malkin, AMNH); Oaxaca, 19 July 1947, 1♀ (B. Malkin, AMNH); San Juan Quiotepec, July 1962, 1♀ (W. S. Miller, AMNH). *Campeche*: Chicanna Ruins, 8 km W Xpujil, 18°32′N, 89°31′W, 12–14 July 1983, 1♀ (W. Maddison, MCZ). *Chiapas*: (Van Patten, MCZ); San

Cristobal de Las Casas, 22 July 1947, 1♂ (C., M. Goodnight, AMNH). GUATEMALA Capetillo, 20–23 Aug. 1947, 1♀ (C., P. Vaurie, AMNH). NICARAGUA *Jinotega*: Jinotega, 15 Aug. 1989, 1♂ (F. Reinboldt, JM); 5 km Jinotega, Los Pinares, 29 May 1992, 1♀ (J. Maes, C. Pineda, JM); Matagalpa, 4 Oct. 1952, 2♀ (R. B. Swain, AMNH); 1 Nov. 1991, 1♀ (J. Maes, JM).

Mangora ixtapan new species
Figures 157–163; Map 2G

Holotype. Female holotype, male paratype, and two female paratypes from 6.5 km W Uruapán, 2,300 m, Michoacan, Mexico, 15 Aug. 1967 (R. E. Leech) in MCZ. The name is a noun in apposition after the locality of a paratype.

Description. Female holotype. Prosoma light orange, except black circles around secondary eyes; distal articles of legs gray. Abdomen orange-white, with spinnerets dark gray (Fig. 160). Posterior eye row straight. Ocular trapezoid longer than wide, rectangular. Posterior median eyes 1.0 diameter of anterior medians; lateral eyes 0.8 diameter. Anterior median eyes 1.0 diameter apart, 1.0 from laterals. Posterior median eyes 0.9 diameter apart, 1.2 from laterals. Height of clypeus equals 0.8 diameter of anterior median eyes. Total length 3.1 mm. Carapace 1.2 mm long, 1.1 wide in thoracic region, 0.6 wide behind lateral eyes, 0.6 high. First femur 1.4 mm, patella and tibia 1.5, metatarsus 1.3, tarsus 0.6. Second patella and tibia 1.4 mm, third 0.8, fourth 1.4.

Male paratype. Prosoma yellow, abdomen lighter yellowish without marks. Posterior eye row recurved. Ocular trapezoid longer than wide, widest anteriorly. Posterior median eyes 1.2 diameters of anterior medians; lateral eyes 0.8 diameters. Anterior median eyes 0.8 diameter apart, 1.0 from laterals. Posterior median eyes 0.3 diameter apart, 1.0 from laterals. Total length 2.3 mm. Carapace 1.2 mm long, 0.9 wide in thoracic region, 0.4 wide behind lateral eyes, 0.4 high. First femur 1.2 mm, patella and tibia 1.3, metatarsus 0.9, tarsus 0.5. Second patella and tibia 1.2 mm, third 0.7, fourth 1.1.

Variation. Total length of females 2.7–3.1 mm. The illustrations were made from female holotype and male paratype.

Diagnosis. The epigynum of *M. ixtapan* is lightly sclerotized and distinguished from others by the semicircular scape (Fig. 157) and a posterior median plate widening toward the scape (Fig. 158).

The palpus of the male, in apical view, differs from that of *M. passiva* and *M. candida* by having the dagger-shaped rod with a right-angle bend (Figs. 161, 163).

Distribution. Michoacan, México, Mexico (Map 2G).

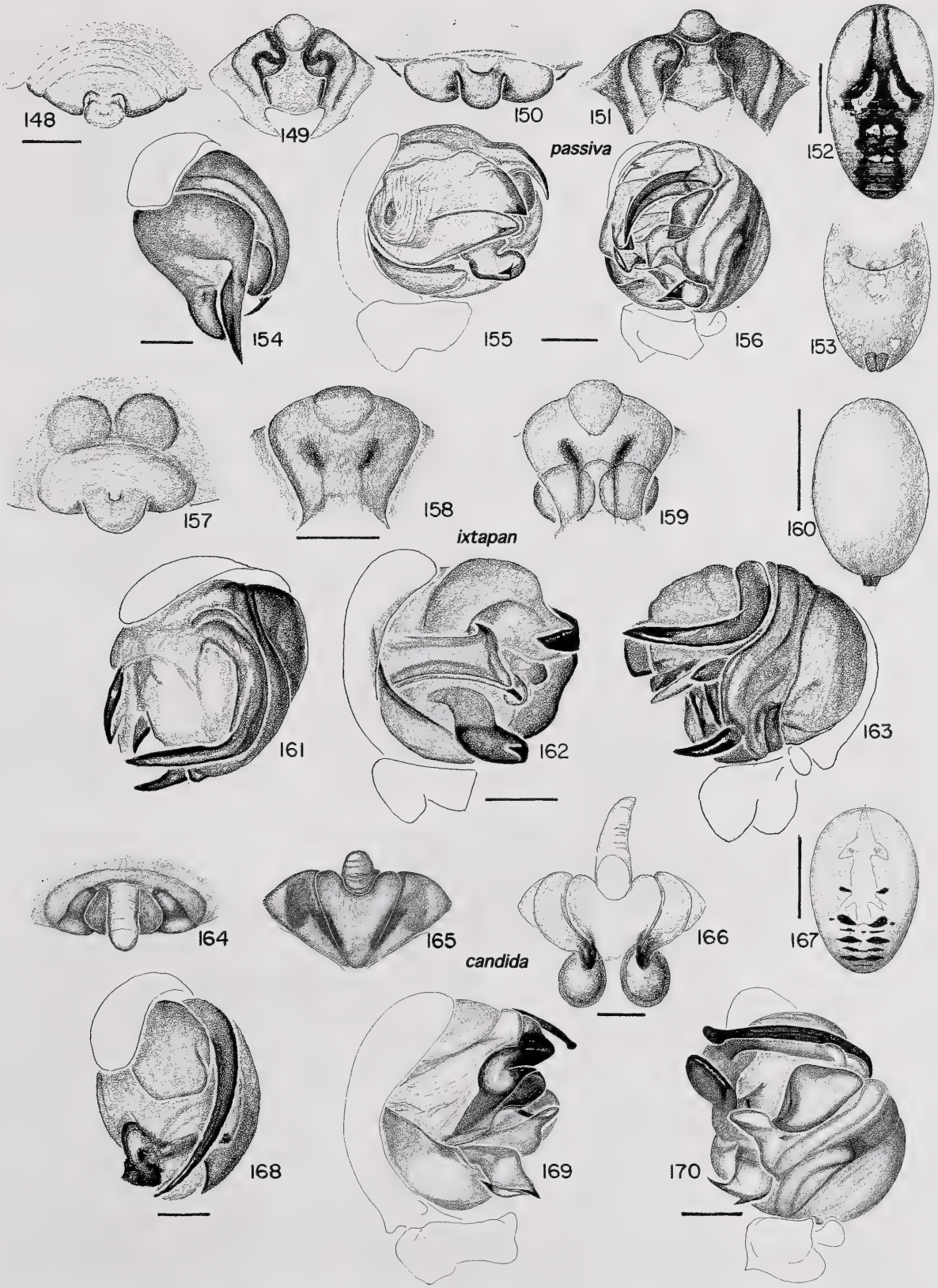
Paratype. MEXICO *México*: Ixtapan de la Sal, 21–28 Aug. 1946, 1♀ (H. Wagner, AMNH).

Mangora candida Chickering
Figures 164–170; Map 2G

Mangora candida Chickering, 1954: 198, figs. 6–9, ♀♂. Male holotype from Barro Colorado Island, Gatun Lake, Panama, in MCZ, examined. Platnick, 2004.

Description. Female from Madden Dam, Panama. Prosoma yellow-white. Abdomen whitish with white pigment spots, and several pairs of black lines posteriorly (Fig. 167). Posterior eye row slightly recurved. Ocular trapezoid longer than wide, widest anteriorly. Posterior median eyes 0.9 diameter of anterior medians; lateral eyes 0.8 diameter. Anterior median eyes 1.0 diameter apart, 0.8 from laterals. Posterior median eyes almost touching, 1.3 diameters from laterals. Height of clypeus equals 0.8 diameter of anterior median eyes. Total length 3.8 mm. Carapace 1.7 mm long, 1.3 wide in thoracic region, 0.6 wide behind lateral eyes, 0.8 high. First femur 1.8 mm, patella and tibia 2.3, metatarsus 1.8, tarsus 0.8. Second patella and tibia 1.8 mm, third 1.2, fourth 2.0.

Male from Madden Dam. Coloration as in female (Fig. 167). Posterior eye row slightly recurved. Ocular trapezoid longer than wide, widest anteriorly. Posterior median eyes 0.8 diameter of anterior medians; lateral eyes 0.5 diameter. Anterior median eyes 0.6 diameter apart, 0.5 from laterals. Posterior median eyes almost touching, 1.0 diameter from laterals. Total



Figures 148–156. *Mangora passiva* (O. P.-Cambridge). 148–153, female. 148–151, epigynum. 148, 150, ventral. 149, 151, posterior. 152, abdomen, dorsal. 153, abdomen, ventral. 154–156, male, left palpus. 154, apical. 155, mesal. 156, ventral.

Figures 157–163. *Mangora ixtapan* new species. 157–160, female. 157–159, epigynum. 157, ventral. 158, posterior. 159, posterior, cleared. 160, abdomen, dorsal. 161–163, male, palpus. 161, apical. 162, mesal. 163, ventral.

Figures 164–170. *Mangora candida* Chickering. 164–167, female. 164–166, epigynum. 164, ventral. 165, posterior. 166, posterior, cleared. 167, abdomen, dorsal. 168–170, male, palpus. 168, apical. 169, mesal. 170, ventral.

Scale lines: 1.0 mm, genitalia 0.1 mm.

length 2.7 mm. Carapace 1.3 mm long, 0.9 wide in thoracic region, 0.4 wide behind lateral eyes, 0.7 high. First femur 1.5 mm, patella and tibia 1.8, metatarsus 1.5, tarsus 0.6. Second patella and tibia 1.4 mm, third 0.8, fourth 1.5.

Variation. Total length of females 3.3–3.8 mm, males 2.2–2.7 mm. The illustrations were made from the holotype and male allotype.

Diagnosis. The epigynum of *M. candida* is lightly sclerotized and distinguished from others by having the long scape flanked by large depressions (Fig. 164), and a triangular, pointed, median posterior plate (Fig. 165). The pattern of the abdomen, with several pairs of black streaks (Fig. 167), is distinctive.

Unlike that of the males of *M. passiva* and *M. sufflava,* the palpus of the male in apical view has a gently curved dagger-shaped rod (Fig. 168) with a distal flattened tip (Fig. 169).

Natural History. Specimens have been collected in forest in Panama.

Distribution. This species is known only from along the Panama Canal area (Map 2G).

Paratypes. PANAMA *Panamá*: Barro Colorado Island, 2 Aug. 1954, 1♂ (A. M. Chickering, MCZ); 1975, 1♂ (W. Eberhard, MCZ); Madden Dam, Aug. 1939, 1♀, 2♂ (A. M. Chickering, MCZ); Forest Reserve, numerous collections (A. M. Chickering, MCZ).

Mangora sufflava Chickering
Figures 171–174; Map 2G

Mangora sufflava Chickering, 1963: 9, figs. 12–15, ♂. Male holotype from Boquete, Chiriquí, Panama, in MCZ, examined. Platnick, 2004.

Note. Chickering did not mention the similarity of this species to *M. passiva* or how they can be separated.

Description. Male holotype. Carapace with a median dusky line, median eye region and clypeus gray. Legs yellowish. Sternum yellowish, gray toward borders. Abdomen yellowish white, dorsally with posterior pair of black rectangles (Fig. 174). Posterior eye row recurved. Ocular trapezoid longer than wide, widest anteriorly. Posterior median eyes 1.0 diameter of anterior medians; lateral eyes 0.8 diameter. Anterior median eyes 0.8 diameter apart, 0.5 from laterals. Posterior median eyes 0.3 diameter apart, 1.0 from laterals. Height of clypeus equal to 0.8 diameter of anterior median eye. Total length 2.6 mm. Carapace 1.3 mm long, 1.1 wide in thoracic region, 0.5 wide behind lateral eyes, 0.7 high. First femur 1.5 mm, patella and tibia 1.6, metatarsus 1.2, tarsus 0.7. Second patella and tibia 1.4 mm, third 0.8. Fourth femur 1.3 mm, patella and tibia 1.2, metatarsus 0.9, tarsus 0.5.

The female is not known.

Diagnosis. The apical view of the palpus differs from that of *M. passiva* (Fig. 154) by having a more gracefully shaped curved rod (Fig. 171), and in mesal view, a heavily sclerotized median apophysis spine (4 h in Fig. 172).

Distribution. Chiriquí, Panama (Map 2G).

Specimens Examined. No other specimens have been found.

Mangora chicanna new species
Figures 175–181; Map 2H

Holotype. Female holotype from Chicanna Ruins, ca. 8 km W of Xpujil, ca. 18°32′N, 89°31′W, Campeche, Mexico, 12–14 July 1983 (W. Maddison) in MCZ. The species is named after the type locality as a noun in apposition.

Description. Female paratype from Honduras. Carapace golden yellow, with small black eye rings. Sternum, legs yellow.

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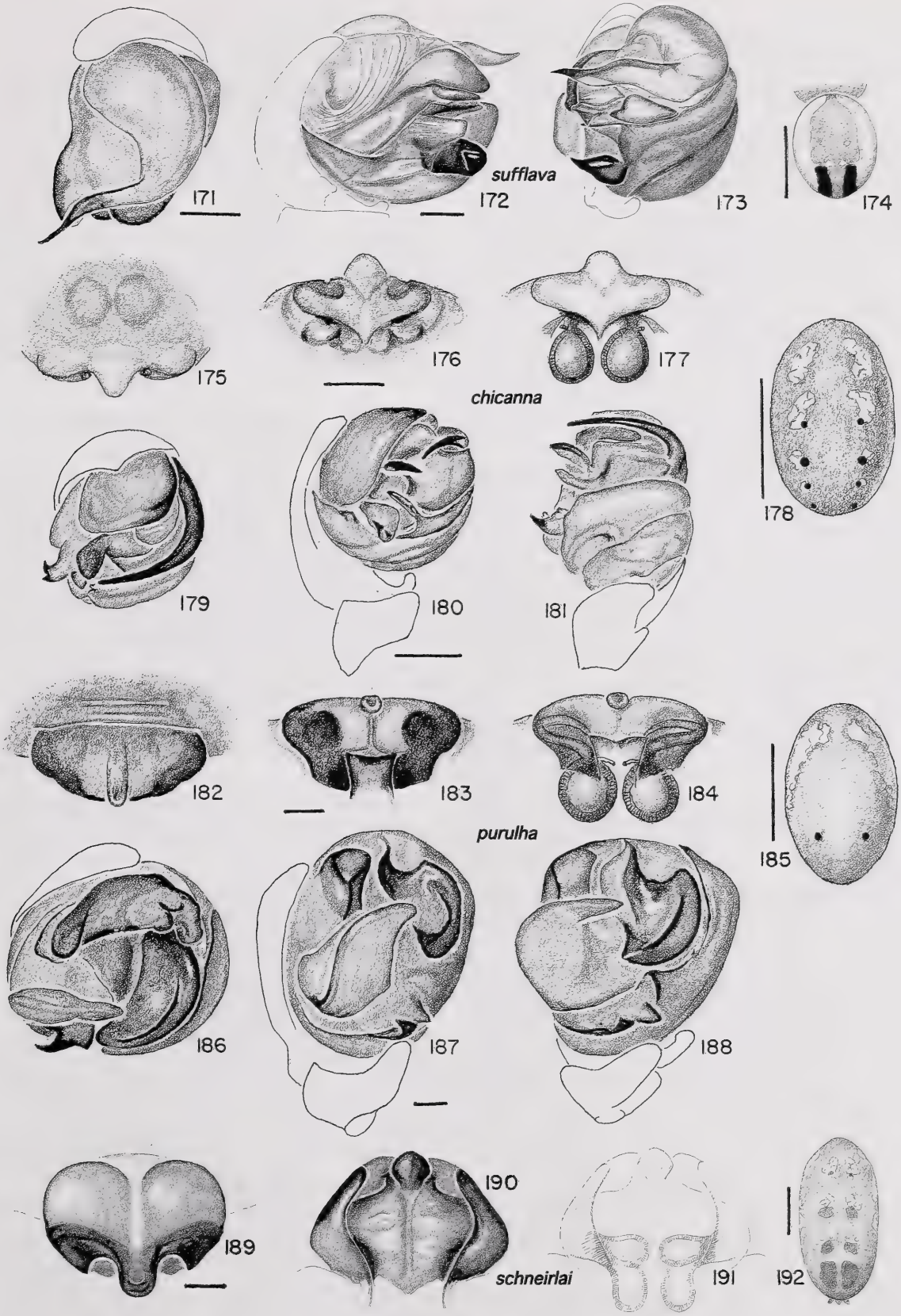
Figures 171–174. *Mangora sufflava* Chickering, male. 171–173, left palpus. 171, apical. 172, mesal. 173, ventral. 174, abdomen, dorsal.

Figures 175–181. *Mangora chicanna* new species. 175–178, female. 175–177, epigynum. 175, ventral. 176, posterior. 177, posterior cleared. 178, abdomen, dorsal. 179–181, male, palpus. 179, apical. 180, mesal. 181, ventral.



Figures 182–188. *Mangora purulha* new species. 182–185, female. 182–184, epigynum. 182, ventral. 183, posterior. 184, posterior, cleared. 185, abdomen, dorsal. 186–188, male, palpus. 186, apical. 187, mesal. 188, ventral.

Figures 189–192. *Mangora schneirlai* Chickering, female. 189–191, epigynum. 189, ventral. 190, posterior. 191, posterior, cleared. 192, abdomen, dorsal.

Scale lines: 1.0 mm, genitalia 0.1 mm.

Abdomen whitish, with pairs of white pigment patches and four pairs of round, black spots (Fig. 178); venter without marks. Posterior eye row procurved. Ocular trapezoid longer than wide, widest anteriorly. Posterior median eyes 0.8 diameter of anterior medians; lateral eyes 0.7 diameter. Anterior median eyes 0.5 diameter apart, 0.5 from laterals. Posterior median eyes 0.3 diameter apart, 1.2 from laterals. Total length 2.4 mm. Carapace 1.2 mm long, 0.8 wide in thoracic region, 0.3 wide behind lateral eyes, 0.5 high. First femur 1.4 mm, patella and tibia 1.6, metatarsus 1.3, tarsus 1.1. Second patella and tibia 1.4 mm, third 0.7, fourth 1.3 mm.

Male paratype from Campeche. All light yellowish, abdomen lighter with four pairs of black spots on abdomen, but no white pigment. Posterior eye row slightly procurved. Eye trapezoid widest in front, as long as wide in front. Posterior median eyes 0.7 diameter of anterior medians; lateral eyes 0.5 diameter. Anterior median eyes 0.7 diameter apart, 0.4 from laterals. Posterior median eyes 0.4 diameter apart, 1.0 from laterals. Total length 2.2 mm. Carapace 1.1 mm long, 0.7 wide in thoracic region, 0.3 wide behind lateral eyes, 0.5 high. First femur 1.3 mm, patella and tibia 1.6, metatarsus 1.2, tarsus 0.5. Second patella and tibia 1.3 mm, third 0.7, fourth 1.2 mm.

Variation. Total length of females 2.2–3.0 mm, males 1.8–2.2 mm. The illustrations of a female were made from a paratype from Honduras, and male allotype from Campeche, Mexico.

Diagnosis. The four pairs of circular, black dots on the abdomen (Fig. 178) easily characterize *M. chicanna.* The epigynum is lightly sclerotized and distinguished from others by the short, wide posterior median plate (Fig. 176).

The palpus of the male, in apical view, differs by having a strongly curved rod (Fig. 179) and the median apophysis has two spines (Figs. 179, 180).

Natural History. Specimens came from dry, deciduous forest in Campeche.

Distribution. Yucatan Peninsula, Chiapas to Honduras (Map 2H).

Paratypes. MEXICO *Campeche*: Reserva de la Biosfera, Calakmul, km 32, 20 July 1998, 1♀, 1♂ (F. Alvarez, MCZ); 26 July 1998, 2♀, 1♂ (F. Alvarez, MCZ). *Yucatan*: Colonia Yucatán, 22 Aug. 1964, 1♀ (J. C. Pallister, AMNH); Progreso, 25 July 1952, 1♀ (J., D. Pallister, AMNH). *Quintana Roo*: Chancanah, Cozumel, 8 Aug. 1949, 1♀ (C. Goodnight, AMNH); San Felipe de Bacalor, 8 July 1993, 1♀ (G. Alayón, ECOSUR); Rancho Las Palmas, 30 km S Felipe Carrillo Puerto, 10 June 1993, 1♂ (G. Alayón, ECOSUR). *Chiapas*: El Real, 6 July 1950, 1♀ (C., M. Goodnight, AMNH). HONDURAS Bouacca Island [?], 1–15 Apr. 1935, 1♀ (M. Bates, MCZ).

Mangora purulha new species
Figures 182–188; Map 2H

Holotype. Female holotype with male paratype from Purulhá, Baja Verapaz, Guatemala, 2,300 m, 23 May 1979 (J. Coddington) in MCZ. The name is a noun in apposition after the type locality.

Description. Female holotype. Prosoma pale orange. Abdomen light orange-white, with a pair of posterior spots and white pigment anterior on sides (Fig. 185); venter orange-white, sides of spinnerets gray. Posterior eye row straight. Ocular trapezoid longer than wide, rectangular. Posterior median eyes 1.2 diameters of anterior medians; lateral eyes 1.0 diameter. Anterior median eyes 1.0 diameter apart, 1.0 diameter from laterals. Posterior median eyes 0.6 diameter apart, 1.1 from laterals. Height of clypeus equals 0.5 diameter of anterior median eyes. Total length 3.2 mm. Carapace 1.4 mm long, 1.2 wide in thoracic region, 0.6 wide behind lateral eyes, 0.7 high. First femur 1.5 mm, patella and tibia 1.8, metatarsus 1.5, tarsus 0.7. Second patella and tibia 1.7 mm, third 1.0. Fourth femur 1.6 mm, patella and tibia 1.6, metatarsus 1.3, tarsus 0.6.

Male paratype. Similar color as female, but white on sides of abdomen more extensive than in female. Posterior eye row straight. Ocular trapezoid longer than wide, widest anteriorly. Posterior median eyes 0.8 diameter of anterior medians; lateral eyes 0.7 diameter. Anterior median eyes 1.2 diameters apart, 1.0 from laterals. Posterior median eyes 1.0 diameter apart,

1.8 from laterals. Total length 2.7 mm. Carapace 1.6 mm long, 1.3 wide in thoracic region, 0.5 wide behind lateral eyes, 0.7 high. First femur 1.6 mm, patella and tibia 1.8, metatarsus 1.6, tarsus 0.7. Second patella and tibia 1.7 mm, third 1.0, fourth 1.7.

Diagnosis. *Mangora purulha* is distinguished by two circular, black dots on the abdomen (Fig. 185). The epigynum differs by a lightly sclerotized, slender scape on a curved, transverse plate (Fig. 182), and in posterior view, by lateral sclerotization (Fig. 183).

Males also have two black spots on the abdomen and the palpus has a median apophysis with one curved spine visible in apical view (Fig. 186), a soft, large embolus (Figs. 187, 188), and a sclerotized terminal apophysis (Fig. 186). Because only one male was available, the sclerites were not carefully examined nor was their homology checked.

Distribution. Guatemala (Map 2H).

Specimens Examined. No other specimens have been found.

Mangora schneirlai Chickering
Figures 189–192; Map 2H

Mangora schneirlai Chickering, 1954: 209, fig. 22, ♀. Female holotype from Barro Colorado Island, Gatun Lake, Panama, in AMNH, examined. Platnick, 2004.

Description. Female paratype. Prosoma yellowish. Abdomen yellowish, with four white spots and a pair of black rectangles posteriorly (Fig. 192); venter with a pair of white spots lateral to genital furrow and lateral to spinnerets. Posterior eye row recurved. Ocular trapezoid slightly longer than wide, widest anteriorly. Posterior median eyes 1.0 diameter of anterior medians; lateral eyes 0.6 diameter. Anterior median eyes 0.8 diameter apart, 0.8 from laterals. Posterior median eyes 0.4 diameter apart, 1.0 from laterals. Legs heavy. Total length 4.8 mm. Carapace 1.7 mm long, 1.0 wide in thoracic region, 0.6 wide behind lateral eyes, 0.7 high. First femur 1.8 mm, patella and tibia 2.0, metatarsus 1.5, tarsus 0.7. Second patella and tibia 1.8 mm, third 1.3. Fourth femur 1.7 mm, patella and tibia 2.0, metatarsus 1.6, tarsus 0.7.

The male is not known.

Variation. Total length of females 3.5–4.8 mm. The illustrations were made from the female holotype.

Diagnosis. *Mangora schneirlai* belongs to the group of species with two black rectangles on the posterior of the abdomen (Fig. 192). The epigynum differs from that of other species with this pattern by having a median scape flanked by a semicircular notch on each side (Fig. 189). The posterior view of the epigynum of *M. schneirlai* (Fig. 190) differs from others, except *M. corcovado,* by having the wide, median plate covered by the narrow lateral ones on each side (Fig. 190).

Distribution. Costa Rica, Panama (Map 2H).

Paratype. PANAMA Panamá, Apr., May 1946, 1♀ (T. C. Schneirla, MCZ).

Specimens Examined. COSTA RICA *Puntarenas*: Corcovado Natl. Park, 11 Aug. 1979, 1♀ (J. Coddington, MCZ). PANAMA *Panamá*: Barro Colorado Isl., Gatun Lake, 30 July, 1964, 1♀ (D. M. Rees, AMNH); nr. Gamboa, Sep. 1975, 2♀ (W. Eberhard, MCZ).

Mangora bimaculata (O. P.-Cambridge)
Figures 193–199; Map 2I

Epeira bimaculata O. P.-Cambridge, 1889: 21, pl. 6, figs. 12, 13, ♀♂. Specimens from between Petet [Petén, El Petén] and Chicoyoito [?], Guatemala, Cahabón [Alto Verapaz], Quiriguá [Izabal], and Veragua, Panama, in BMNH, examined. Keyserling, 1893: 260, pl. 13, fig. 19, ♀♂.

Mangora bimaculata:—F. O. P.-Cambridge, 1904: 479, pl. 45, figs. 10, 11, ♀♂. Chickering, 1954: 197, figs. 1–5, ♀♂. Platnick, 2004.

Description. Female from Petén, Guatemala. Prosoma yellowish. Abdomen whitish with white pigment spots and a pair of dorsal posterior black rectangles (Fig. 196); venter with white pigment spots except in midline. Posterior eye row recurved. Ocular trapezoid as long as wide in front, widest anteriorly. Posterior median eyes 1.0 diameter of anterior medians; lateral eyes 0.7 diameter. Anterior me-

dian eyes 0.4 diameter apart, 1.2 from laterals. Posterior median eyes 0.2 diameter apart, 1.5 from laterals. Total length 6.3 mm. Carapace 2.2 mm long, 1.8 wide in thoracic region, 0.8 wide behind lateral eyes, 1.2 high. First femur 2.7 mm, patella and tibia 3.0, metatarsus 2.6, tarsus 1.1. Second patella and tibia 2.7 mm, third 1.7, fourth 2.9.

Male from Hidalgo, Mexico. Prosoma light orange. Abdomen as in female. Posterior eye row procurved. Ocular trapezoid longer than wide, widest anteriorly. Posterior median eyes 0.9 diameter of anterior medians; lateral eyes 0.8 diameter. Anterior median eyes 1.0 diameter apart, 0.3 from laterals. Posterior median eyes almost touching, 0.8 from laterals. Total length 2.3 mm. Carapace 1.2 mm long, 0.9 wide in thoracic region, 0.4 wide behind lateral eyes, 0.7 high. First femur 1.3 mm, patella and tibia 1.5, metatarsus 1.2, tarsus 0.7. Second patella and tibia 1.3 mm, third 0.7, fourth 1.2.

Variation. Total length of females 5.3–6.3 mm. A female from Chiapas has indistinct black bands rather than patches on the abdomen. The illustrations were made from female and male syntypes; Figure 197 was from a Hidalgo male.

Diagnosis. Mangora bimaculata differs from sympatric species in the north by the coloration of the abdomen and from those with similar abdomen patches by the epigynum, which is heavily sclerotized and has an oval posterior opening with an anterior median tubercle (Fig. 193); in posterior view the median plate forms a groove (Fig. 194).

The palpus of the male differs from that of *M. sufflava* by the different shape of the terminal apophysis, having a shorter, distal dagger-shaped rod (Fig. 197).

Natural History. Specimens from Barrancas came from a palm forest; the Chiapas specimens were collected by sweeping.

Distribution. Central Mexico to Costa Rica (Map 2I).

Specimens Examined. MEXICO *Hidalgo*: 3.2 km SW Jacala, 18 Aug. 1964, 1♂ (J., W. Ivie, AMNH). *Chiapas*: Palenque Ruins, 9 July 1949, 1♀ (C. J. Goodnight, AMNH). GUATEMALA *Petén*: Uaxactún, Mar.–Apr. 1931, 1♀ (H. H. Bartlett, MCZ). COSTA RICA *San José*: San Isidro del General, 600–1,200 m, 1♀ (D. Rounds, MCZ). *Puntarenas*: Barrancas, 13 June 1979, 1♀ (J. Coddington, MCZ).

Mangora pia Chamberlin and Ivie
Figures 200–207; Map 2J

Mangora pia Chamberlin and Ivie, 1936: 58, pl. 12, fig. 112, ♀. Female holotype from Barro Colorado Island, Panama, in AMNH, examined. Chickering, 1954: 208, figs. 18–21, ♀♂. Platnick, 2004.

M. belligerens Chamberlin and Ivie, 1936: 60, pl. 12, fig. 113, ♂. Male holotype from Barro Colorado Island, Panama, in AMNH, examined. First synonymized with *pia* by Chickering, 1954.

M. wiedenmeyeri Schenkel, 1953: 18, fig. 15, ♀. Female holotype from El Pozón, Depto. Acosta, Falcón, Venezuela, in NMB, examined. Platnick, 2004. NEW SYNONYMY.

Description. Female from Barro Colorado Island. Prosoma light orange. Abdomen whitish, with a pair of posterior black rectangles and indistinct longitudinal lines with white pigment spots (Fig. 203); venter whitish with a pair of white spots, one on each side anterior to spinnerets, and two indistinct longitudinal lines of white pigment spots. Posterior eye row straight. Ocular trapezoid longer than wide, widest anteriorly. Posterior median eyes 0.8 diameter of anterior medians; lateral eyes 0.6 diameter. Anterior median eyes 0.7 diameter apart, 1.0 from laterals. Posterior median eyes 0.4 diameter apart, 1.4 from laterals. Total length 5.5 mm. Carapace 2.4 mm long, 2.0 wide in thoracic region, 0.8

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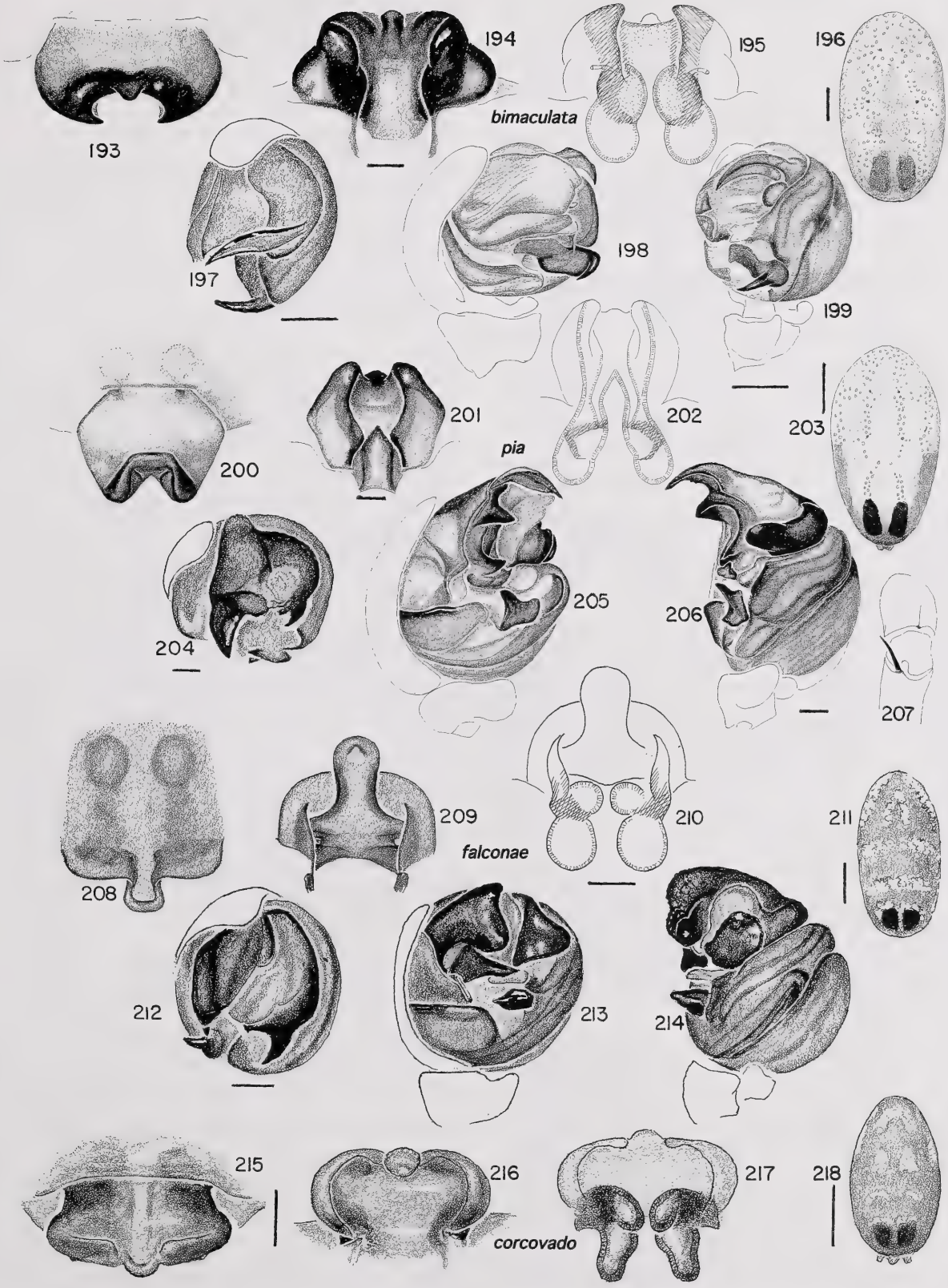
Figures 193–199. *Mangora bimaculata* (O. P.-Cambridge). 193–196, female. 193–195, epigynum. 193, ventral. 194, posterior. 195, posterior, cleared. 196, abdomen, dorsal. 197–199, male, left palpus. 197, apical. 198, mesal. 199, ventral.

Figures 200–207. *Mangora pia* Chamberlin and Ivie. 200–203, female. 200–202, epigynum. 200, ventral. 201, posterior. 202, posterior, cleared. 203, abdomen, dorsal. 204–207, male. 204–206, palpus. 204, apical. 205, mesal. 206, ventral. 207, proximal end of fourth leg, ventral.



Figures 208–214. *Mangora falconae* Schenkel. 208–211, female. 208–210, epigynum. 208, ventral. 209, posterior. 210, posterior, cleared. 211, abdomen, dorsal. 212–214, male, palpus. 212, apical. 213, mesal. 214, ventral.

Figures 215–218. *Mangora corcovado* new species, female. 215–217, epigynum. 215, ventral. 216, posterior. 217, posterior, cleared. 218, abdomen, dorsal.

Scale lines: 1.0 mm, genitalia 0.1 mm.

wide behind lateral eyes, 1.4 high. First femur 3.0 mm, patella and tibia 3.2, metatarsus 3.0, tarsus 1.1. Second patella and tibia 3.1 mm, third 2.1. Fourth femur 3.2 mm, patella and tibia 3.3, metatarsus 2.8, tarsus 1.1.

Male from Barro Colorado Island, Panama. Coloration as in female. Posterior eye row straight. Eye trapezoid longer than wide, widest anteriorly. Posterior median eyes 0.8 diameter of anterior medians; anterior lateral eyes 0.7 diameter, posterior 0.6. Anterior median eyes 0.8 diameter apart, 0.8 from laterals. Posterior median eyes 0.2 diameter apart, 1.2 from laterals. Fourth femur with a proximal, ventral macroseta (Fig. 207). Total length 3.8 mm. Carapace 2.0 mm long, 1.8 wide in thoracic region, 0.7 wide behind lateral eyes, 1.0 high. First femur 2.3 mm, patella and tibia 2.6, metatarsus 2.3, tarsus 0.9. Second patella and tibia 2.2 mm, third 1.5, fourth 2.4.

Variation. Total length of females 5.0–6.7 mm, males 3.3–4.3 mm. The illustrations were made from the female holotype of *M. pia*: Figures 205 and 206 were from the holotype of *M. belligerens*; and Figure 204 was from a specimen from Barro Colorado Island, Panama.

Diagnosis. Mangora pia differs from females of other species with a pair of black rectangles on the abdomen by the distinctive heavily sclerotized epigynum, which has a median, triangular notch, framed by a sclerotized fold (Fig. 200).

Males differ from males of *M. melanocephala* and *M. falconae* (which also have a macroseta on the venter of the proximal end of the fourth femur; Fig. 207), by being much larger in size than *M. melanocephala* and lacking the filamentous embolus in the palpus (Figs. 205–206), and from *M. falconae,* in apical view, by the thick spine of the terminal apophysis (Fig. 204).

Natural History. Living specimens are green (Craig, personal communication). Specimens have been found in forest in Panama. *Mangora pia* "is a wet season, forest understory spider and the ones I worked on lived in vegetation near streams but not on the stream edge. They build very delicate and beautiful webs, densely spun, and the viscid silk is extremely stretchy and densely coated with glue" (Craig, personal communication). Lubin (1978) writes that the species is primarily diurnal but complete webs can be found at night.

Distribution. Panama, northern Venezuela and eastern Colombia (Map 2J).

Specimens Examined. PANAMA Taboga Isl., 23 Aug. 1946, 1♀ (N. L. H. Krauss, AMNH). *Panamá*: Araijan, Cerro Galero, very common (W. Eberhard, MCZ); Barro Colorado Island, Gatun Lake, very common (AMNH, MCZ, USNM); Cocoli area, July–Sep. 1954, 2♀ (W. E. Lundy, AMNH); France Field, Aug. 1939, 1♂ (A. M. Chickering, MCZ); Pedro Miguel, July 1950, 1♀ (A. M. Chickering, MCZ); Experimental Gardens, 11–13 July 1954, 1♀, 2♂ (A. M. Chickering, MCZ); Forest Reserve, Aug. 1939, 2♂; July 1950, 1♂ (A. M. Chickering, MCZ); Parque Nac. Soberiana, 7 Aug. 1983, 2♀ (R. J. Raven, AMNH); Pipe line Road nr. Gamboa, 6 Jan. 1977, 1♀ (H. Levi, M. Robinson, MCZ); Chilibre, July 1950, 1♂ (A. M. Chickering, MCZ); Madden Dam, Aug. 1939, 1♀ (A. M. Chickering, MCZ); Fort Knobbe, 3 Aug. 1983, 1♀ (H., L. Levi et al., MCZ); Summit, Nov. 1946, 1♀ (N. L. H. Krauss, AMNH); Summit Gardens, July 1954, 1♀ (A. M. Chickering, MCZ); El Valle, 3♀ (A. M. Chickering, MCZ); Villa Darién, 12–28 Feb. 1984, 2♀ (M. N. García, MIUP). COLOMBIA *Valle*: nr. Cali, 1,000 m, 3♀ (W. Eberhard 1128, 1131, 1132, MCZ); Río Jamundi nr. Jamundi, 9 Dec. 1969, 1♀ (W. Eberhard, MCZ).

Mangora falconae Schenkel
Figures 208–214; Map 2K

Mangora falconae Schenkel, 1953: 19, fig, 17, ♀. Female holotype from El Pozón, Depto. Acosta, Falcón, Venezuela, in NMB, examined. Platnick, 2004.

Description. Female from Magdalena, Colombia. Prosoma light orange. Abdomen orange-white, with two posterior black rectangles and streaks of white pigment spots (Fig. 211); venter orange-white. Posterior eye row straight. Ocular trapezoid longer than wide, slightly widest anteriorly. Posterior median eyes 0.8 diameter of anterior medians; lateral eyes 0.7 diameter. Anterior median eyes 0.5 diameter apart, 0.8 from laterals. Posterior

median eyes 0.3 diameter apart, 1.2 from laterals. Total length 4.3 mm. Carapace 1.8 mm long, 1.5 wide in thoracic region, 0.7 wide behind lateral eyes, 1.3 high. First femur 2.1 mm, patella and tibia 2.1, metatarsus 1.6, tarsus 0.6. Second patella and tibia 1.8 mm, third 1.3. Fourth femur 2.1 mm, patella and tibia 2.2, metatarsus 1.7, tarsus 0.7.

Male from Magdalena, Colombia. Coloration as in female, except venter of abdomen with a large, median patch of white pigment spots. Posterior eye row slightly recurved. Ocular trapezoid longer than wide, widest anteriorly. Posterior median eyes 0.8 diameter of anterior medians; lateral eyes 0.6 diameter. Anterior median eyes 0.4 diameter apart, 0.4 from laterals. Posterior median eyes 0.3 diameter apart, 1.0 from laterals. Height of clypeus equal to 0.8 diameter of anterior median eye. Fourth femur with proximal, ventral macroseta (Fig. 207). Total length 2.8 mm. Carapace 1.8 mm long, 1.2 wide in thoracic region, 0.5 wide behind lateral eyes, 0.7 high. First femur 1.6 mm, patella and tibia 1.7, metatarsus 1.3, tarsus 0.6. Second patella and tibia 1.4 mm, third 0.9, fourth 1.5.

Variation. Total length of females 3.1–4.4 mm, males 2.6–2.8 mm. The illustrations were made from the female holotype, and from a male specimen from Colombia.

Diagnosis. The epigynum of *M. falconae* is distinct from that of all species in having a pair of black rectangles on the abdomen, by the scape having a narrow base (Fig. 208), and in posterior view having the median plates upside-down-T–shaped (Fig. 209).

Males are distinguished from those of *M. melanocephala* and *M. pia*, which also have a macroseta on the fourth femur (Fig. 207), by a palpus with the terminal apophysis having a thorn-shaped hook seen in apical view (Fig. 212).

Natural History. Specimens have been collected on plants in Colombia, and from a coastal thorn-scrub in Venezuela.

Distribution. Panama, northern Venezuela, Colombia (Map 2K).

Specimens Examined. PANAMA *Chiriquí*: 1938, 1♀ (AMNH).

VENEZUELA *Sucre*: Carúpano, 23–31 July 1987, 1♂ (S., J. Peck, AMNH). COLOMBIA *Magdalena*: Tayrone Park, Gairaca, 8 km NE Santa Marta, 13 June 1985, 1♀ (H.-G. Müller, SMF); Tayrone Park, 16 km NE Santa Marta, 16 June 1985, 9♀, 1♂, 2 imm. (H.-G. Müller, SMF).

Mangora corcovado new species
Figures 215–218; Map 2K

Holotype. Female holotype from Llocona [?]. Corcovado National Park, Puntarenas, Costa Rica, 11 Aug. 1979 (J. Coddington), in MCZ. The name is a noun in apposition after the name of the type locality.

Description. Female holotype. Prosoma yellowish. Abdomen yellowish white with a pair of black rectangles posteriorly, and areas of white spots anteriorly (Fig. 218); venter without marks. Posterior eye row procurved. Ocular trapezoid longer than wide, widest anteriorly. Posterior median eyes 1.0 diameter of anterior medians; lateral eyes 0.6 diameter. Anterior median eyes 0.3 diameter apart, 0.5 from laterals. Posterior median eyes 0.2 diameter apart, 1.0 from laterals. Total length 3.2 mm. Carapace 1.7 mm long, 1.3 wide in thoracic region, 0.6 wide behind lateral eyes, 1.2 high. First femur 1.6 mm, patella and tibia 2.0, metatarsus 1.4, tarsus 0.7. Second patella and tibia 1.8 mm, third 1.3. Fourth femur 1.8 mm, patella and tibia 1.9, metatarsus 1.5, tarsus 0.7.

The male is not known.

Diagnosis. The scape of the epigynum of *M. corcovado* is a short lobe without constriction (Fig. 215) compared to the longer, constricted scape of *M. falconae* (Fig. 208) and in posterior view the epigynum has a wider median plate (Fig. 216) than in *M. falconae*.

Distribution. Costa Rica (Map 2K).

Specimens Examined. No other specimens have been found.

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The Snake Genus *Sibynomorphus* (Colubridae: Dipsadinae: Dipsadini) in Peru and Ecuador, with Comments on the Systematics of Dipsadini

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THE SNAKE GENUS *SIBYNOMORPHUS* (COLUBRIDAE: DIPSADINAE: DIPSADINI) IN PERU AND ECUADOR, WITH COMMENTS ON THE SYSTEMATICS OF DIPSADINI

JOHN E. CADLE[1]

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ABSTRACT. *Sibynomorphus,* an assemblage of about a dozen species of South American gastropod-eating colubrids, has a peculiar distribution. Six species occur in northern Peru and southwestern Ecuador. The others are distributed south of the Amazon basin in Brazil, Bolivia, Paraguay, Uruguay, and Argentina. Species of *Sibynomorphus* known from Ecuador and Peru are reviewed. *Sibynomorphus oligozonatus* and *S. petersi* are reported from Peru for the first time. Study of existing collections considerably amplifies understanding of the geographic ranges and character variation within *S. oligozonatus, S. oneilli, S. petersi,* and *S. williamsi. Sibynomorphus vagrans* is known only from its type locality (Bellavista, Cajamarca Department, Peru), and *S. vagus* (type locality unknown) is known only from near the single historically reported locality for the species (Huancabamba, Piura Department, Peru). *Sibynomorphus oligozonatus* (four specimens known) is distributed in southwestern Ecuador (Azuay and Loja Provinces) and northern Peru (Piura Department). *Sibynomorphus oneilli* is distributed in the Cordillera Oriental and Cordillera Occidental of northern Peru from southern Ancash Department to southern Cajamarca and Amazonas Departments. Available specimens of *S. petersi* extend the known range from Azuay and Loja Provinces in southwestern Ecuador, along the western Andean slopes to southern Ancash Department, Peru (Pacific versant); a single specimen is also known from the upper Río Chotano in central Cajamarca Department, thus documenting that this species occurs on the Amazonian versant. *Sibynomorphus williamsi* is known from central Peru in Lima and Ancash Departments from near sea level to at least 2,900 m in the Andes (and perhaps as high as 3,600 m)—an elevational range unmatched in any other species of the genus. Two species (*S. vagrans* and *S. vagus*) are restricted to the Amazonian versant, two are restricted to the Pacific versant (*S. oligozonatus* and *S. williamsi*), and two are found on both versants (*S. oneilli* and *S. petersi*). A key to the species of *Sibynomorphus* in Peru and Ecuador is provided.

Hemipenes are described for *Sibynomorphus oligozonatus, S. petersi, S. vagrans, S. vagus,* and *S. williamsi.* Their organs are similar to hemipenes of other Dipsadini in having a well-defined capitulum ornamented with papillate calyces, several rows of large spines encircling the organ proximal to the capitulum, an exceptionally large basal nude pocket, and the di-

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vision of the sulcus spermaticus within the capitulum. In *Sibynomorphus* and in some other Dipsadini the branches of the sulcus spermaticus are centrolineal, but their tips pass somewhat to the lateral surface of the hemipenial lobe(s). The exceptional size of the nude pocket might be a synapomorphy of Dipsadini but further comparative studies are needed, especially because the pocket has probably been overlooked in many species.

The natural history of all northern species of *Sibynomorphus* is summarized, but very little is known. Most localities are in relatively dry to arid habitats, such as dry deciduous forests or thorn forests, on the western Andean slopes or inter-Andean valleys. A few localities for *S. petersi* in northern Peru are in areas of mesic to humid forests, although specimens are from forest edge or ecotones in this area. *Sibynomorphus williamsi* is characteristic of the lomas formations on the central Peruvian coast, but it also occurs on the Andean slopes at higher elevations.

Sibynomorphus shares with three other genera of Neotropical Dipsadinae (*Dipsas, Sibon, Tropidodipsas*) a behavioral propensity and associated morphological characteristics for consuming gastropods. In accordance with some previous authors, I suggest that the name Dipsadini be applied inclusively to this clade of four genera of Neotropical molluscivorous colubrids, notwithstanding previous arguments for excluding *Tropidodipsas*. Several external characters indicate that *Sibynomorphus* is most closely related to *Dipsas* within Dipsadini. Nonetheless, the monophyly of *Sibynomorphus* has not been demonstrated and the possibility remains that *Dipsas* is paraphyletic with respect to *Sibynomorphus,* which itself is conceivably polyphyletic. The peculiar distribution of *Sibynomorphus* is somewhat similar to other components of the herpetofauna of southern Ecuador and northern Peru (Andes, Pacific versant, and coast). However, *Sibynomorphus* as presently understood lacks some geographic components (e.g., Amazonia, Guayana) associated with these other taxa.

Some investigations have suggested that *Sibynomorphus* be synonymized with *Dipsas,* but analytical issues such as taxon and character sampling are problematic with previous studies. None of the northern species of *Sibynomorphus* have been included in broader comparative studies. I advocate a broader survey of nominal taxa of Dipsadini before making further changes in the generic nomenclature in this group. Some outstanding questions concerning the systematics and natural history of *Sibynomorphus* are outlined. Especially needed are more detailed studies of microhabitat occurrence and behavior of all species and field studies to further delineate their distributions. The significance of exceptional color pattern variation that occurs within *S. oneilli, S. petersi,* and *S. vagus* needs to be explored, perhaps in conjunction with their role as potential mimics of sympatric species of *Bothrops* (Viperidae). Similarly, the extensive variation in scutellation that occurs generally in many Dipsadini needs functional, mechanistic, and evolutionary explanation.

RESUMEN. *Sibynomorphus,* un grupo de aproximadamente una docena de especies de colubridos sudamericanos que comen gasterópodos, tiene una distribución extraña. Seis especies occuren en el norte del Perú y el Ecuador sudoccidental y los demás son distribuidas al sur de la cuenca Amazónica en Brazil, Bolivia, Paraguay, Uruguay, y Argentina. Se revisan las especies de *Sibynomorphus* de Ecuador y Perú. Se reportan para la primera vez *S. oligozonatus* y *S. petersi* del Perú. El estudio de colecciones que existe aumenta considerablemente el conocimiento de los rangos geográficos y la variación de carácteres de *S. oligozonatus, S. oneilli, S. petersi,* y *S. williamsi.* Todavía se conoce *S. vagrans* solamente de su localidad típica (Bellavista, Departamento de Cajamarca, Perú), y se conoce *S. vagus* (localidad típica desconocida) solamente cercana a la única localidad histórica para la especie (Huancabamba, Departamento de Piura, Perú). *Sibynomorphus oligozonatus* (conocido de cuatro especímenes) se distribuido en el suroeste de Ecuador (provincias Azuay y Loja) y el norte de Perú (departamento de Piura). *Sibynomorphus oneilli* se distribuido en la Cordillera Oriental y la Cordillera Occidental del norte del Perú desde el sur del departamento de Ancash hasta el sur de los departamentos Cajamarca y Amazonas. Los especímenes disponibles de *S. petersi* se extiende el rango conocido desde las provincias Azuay y Loja en el suroeste de Ecuador, a lo largo de las vertientes andinas occidentales hasta el sur del departamento de Ancash, Perú (vertiente Pacífico); un espécimen único se conoce también del alto Río Chotano en el centro del departamento de Cajamarca, que documenta que esta especie también se encuentra en la vertiente Amazónica. *Sibynomorphus williamsi* se conoce del Perú central en los departamentos Lima y Ancash desde cerca del nivel del mar hasta a menos 2,900 m en los Andes (y quizás tan alto como 3,600 m)—un rango elevational incomparable en algún otra especie del género. Dos especies (*S. vagrans* y *S. vagus*) son restringidas a la vertiente Amazónica, dos especies son restringidas a la vertiente Pacífica (*S. oligozonatus* y *S. williamsi*), y dos especies se encuentran en las dos vertientes (*S. oneilli* y *S. petersi*). Se presenta un clave para las especies de *Sibynomorphus* en Perú y Ecuador.

Se describe los hemipenes de *Sibynomorphus oligozonatus, S. petersi, S. vagrans, S. vagus,* y *S. williamsi.* Sus órganos son similar a los hemipenes de otros Dipsadini al tener un capítulo bien definido y ornamentada con cálices que llevan papilas, una serie de espinas grandes que rodean el órgano proximal al capítulo, un excepcionalmente grande bolsillo desnudo basal, y un surco espermático que divide dentro del capítulo. En *Sibynomorphus* y algunas otras especies de Dipsadini las ramas del surco espermático son centrolineal pero sus puntas pasan un tanto al lado lateral del lóbulo(s) del hemipene. El tamaño

excepcional del bolsillo desnudo puede ser una sinapomorfía de Dipsadini pero se necesitan más estudios comparativos, especialmente dado que el bolsillo se ha pasado por alto en muchas especies.

Se resumen la historia natural de todas especies septentrionales de *Sibynomorphus* pero se conoce muy poca de estas especies. La mayoría de las localidades son en hábitats relativamente secos o áridos, tal como bosques caducifolios o bosques espinales, sobre las vertientes occidentales andinas o en valles interandinos. Unas pocas localidades para *S. petersi* en el norte del Perú son en áreas de bosques húmedos o muy húmedos, aunque los ejemplares son del borde de los bosques o los ecotonos en esta región. *Sibynomorphus williamsi* es caracteristico de las lomas en la costa central del Perú pero también se ocurre en las vertientes andinos a elevaciones más altas.

Sibynomorphus comparte con tres otros géneros neotropicales de Dipsadinae (*Dipsas, Sibon,* y *Tropidodipsas*) una propensión conductual y características morfológicas asociadas para consumir gasterópodos. De acuerdo con algunos autores anteriores, sugero que el nombre Dipsadini sea aplicado inclusivamente a este clado de cuatro géneros de colubridos neotropicales moluscivoros, no obstante razones anteriores para excluir *Tropidodipsas.* Varias características externales indican que *Sibynomorphus* es relacionado más cercano a *Dipsas* entre los Dipsadini. Sin embargo, la monofilia de *Sibynomorphus* no se ha sido demostrado y queda la posibilidad que *Dipsas* es parafilético respecto a *Sibynomorphus,* que sí mismo puede ser polifilético. La distribución extraña de *Sibynomorphus* es algo similar a otros componentes de la herpetofauna del sur de Ecuador y el norte del Perú (Andes, vertientes Pacíficas, y la costa). Sin embargo, la distribución de *Sibynomorphus,* en cuanto al entendimiento actual, carece de algunos componentes geográficos (p.e., Amazonia, Guayana) asociados con estos otros taxones.

A pesar de algunos estudios que sugeren que *Sibynomorphus* pase al sinonimia de *Dipsas,* algunos asuntos analíticos, inclusive cuestiones de muestreo de caracteres y taxones, son problemáticos con estudios anteriores. Ninguno de las especies septentrionales de *Sibynomorphus* han sido incluidos en estudios comparativos amplios. Recomendo un estudio más amplio de especies nominales de Dipsadini antes que iniciar más cambios en la nomenclatura genérica de este grupo. Se explica algunas cuestiones pendientes acerca de la sistemática y la historia natural de *Sibynomorphus.* Especialmente se necesitan estudios más detallados de los microhábitas y comportamiento de todas especies y estudios de campo para refinar sus distribuciones geográficas. Se necesita explorar la importancia de la variación excepcional de patrones de coloración en *S. oneilli, S. petersi,* y *S. vagus,* tal vez conjunto con su rol como mímicos potenciales de especies simpátricas de *Bothrops* (Viperidae). Igualmente, la variación extensa en escamación que ocurre generalmente en Dipsadini necesita explicación en términos funcionales, mecanicistos, y evolutivos.

INTRODUCTION

Recent investigations clarified the systematics and distributions of several species of snakes of the genus *Dipsas* (Colubridae: Dipsadinae: Dipsadini[2]) in Panama and northern South America (Cadle, 2005; Cadle and Myers, 2003; Fernandes et al., 2002). Nonetheless, despite Peters' comprehensive review of Dipsadini (Peters, 1960), much additional work is needed on the systematics of this group. This is nowhere more apparent than in the endemic South American genus *Sibynomorphus,* which comprises about a dozen currently recognized species (Franco et al., 2002, 2003; Hoge et al., "1978/1979" [1981]; Peters and Orejas-Miranda, 1970; Scrocchi et al., 1993).

Sibynomorphus has a peculiar distribution. Six or seven species are distributed south of the Amazon in Argentina, Brazil, Paraguay, Uruguay, and Bolivia.[3] The other six species are found along the coast of central Peru; the western Andean foothills of northern Peru and southwestern Ecuador; or the Andes and inter-Andean valleys of the Río Marañón, the Río Santa, and their tributaries in northern Peru (Amazonian and Pacific versants, respectively). Thus, the range of the genus is disjunct

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[2] Dipsadini is here used for snakes of the genera *Dipsas, Sibon, Tropidodipsas,* and *Sibynomorphus,* essentially equivalent to the Dipsadinae of Peters (1960) with the addition of *Tropidodipsas.* See later herein: Sibynomorphus *and the Dipsadini: Directions for Further Research.*

[3] These include *Sibynomorphus inaequifasciatus, S. lavillai, S. mikanii, S. neuwiedii, S. turgidus,* and *S. ventrimaculatus* (Hoge et al., "1978/1979" [1981]; Peters, 1960; Scrocchi et al., 1993). Additionally, *S. garmani* (Cope), previously considered a synonym of *S. mikanii,* was apparently resurrected in an unpublished thesis that I have not seen (Franco, 1994); the name appears in two online abstracts (Franco et al., 2002, 2003). *Sibynomorphus inaequifasciatus* Duméril, Bibron, and Duméril, is known only from the original description. The holotype, said to be "doubtfully from Brazil but certainly from South America," has not been located (Peters, 1960: 146–148).

and the northern and southern species occupy distinct physiographic and climatic zones. Scrocchi et al. (1993) briefly reviewed the species of *Sibynomorphus* from southern South America, but species from Peru and Ecuador remain poorly known and have not received comprehensive review because most were described subsequent to Peters' (1960) work on the group. The lack of a modern review has led to inaccurate identifications of museum material and misunderstandings concerning their distributions.

As recently as the 1960s, when the systematics of *Sibynomorphus* was last reviewed (Peters, 1960; Peters and Orejas-Miranda, 1970), the genus was unreported from Ecuador, and only *S. vagus* (Jan, 1863) and *S. vagrans* (Dunn, 1923) were known from Peru (but see later comments on the name *Leptognathus atypicus* Cope).[4] Jan (1863) had described *Leptognathus vagus* from a specimen said to be from "Hong Kong." This name has been applied to a species from near the town of Huancabamba in northern Peru (Piura Department), known primarily from a series in the Museum of Comparative Zoology collected by G. K. Noble (Dunn, 1923) and a later series from near the same locality (Rossman and Kizirian, 1993). Dunn (1923) described *Pseudopareas vagrans* from specimens collected by Noble in the inter-Andean valley of the upper Río Marañón of northern Peru (Bellavista, Cajamarca Department), and the type series comprises the only known specimens. Both of these earliest described northern species of *Sibynomorphus* are from inter-Andean valleys on the Amazonian versant of the Andes at the western limits of the Amazon basin.

Since 1970, two additional species of *Sibynomorphus* from Peru and two from southern Ecuador have been described: *Sibynomorphus williamsi* Carrillo de Espinoza (1974) from coastal Lima Department, Peru (type locality: Jicamarca); *S. oneilli* Rossman and Thomas (1979) from Amazonas Department, Peru (type locality: between Balsas and Abra Chanchillo); *S. oligozonatus* Orcés and Almendáriz (1989) from Azuay Province, Ecuador (type locality: Zhila); and *S. petersi* Orcés and Almendáriz (1989) from Azuay and Loja Provinces, Ecuador (type locality: Zhila, Azuay Province). Few specimens have been reported for most of the northern species of *Sibynormorphus. Sibynomorphus oligozonatus* and *S. oneilli* were described only on the basis of their holotypes and until now *S. oligozonatus* has been known only from the type. Rossman and Kizirian (1993) reported two additional specimens of *S. oneilli* from Cajamarca Department, Peru, and additional specimens of *S. vagus* from near the previously known locality. *Sibynomorphus petersi* has been known only from three specimens reported in the original description. Of the species of *Sibynomorphus* described since 1970, three (*S. williamsi, S. oligozonatus,* and *S. petersi*) have heretofore been known only from the Pacific versant, and *S. oneilli* only from the Amazonian versant.

Even considering the recently described species, it is clear that the species limits and distributions of *Sibynomorphus* in Ecuador and Peru are incompletely understood. As part of biological surveys in northern Peru (Cadle, 1989, 1991, 1998, 2005; Cadle and Chuna, 1995; Cadle and McDiarmid, 1990; Cadle and Myers, 2003), I obtained a few specimens of *Sibynomorphus,* prompting me to review the species known from Peru and Ecuador. The results of that review form the basis of this report.

Although the accumulated material improves our understanding of variation and the distributions of some taxa, some outstanding problems remain. Nonetheless, a comprehensive review of these species is needed to facilitate future systematic work

[4] Peters (1960: 57–58) synonymized *Sibynomorphus macedoi* Prado and Hoge (1947; type locality: Pucallpa, Ucayali Department, Peru) with *Dipsas catesbyi,* a conclusion I accept without having seen the type.

on this group. In this report, I document the occurrence of *S. oligozonatus* and *S. petersi* in Peru and the presence of *S. petersi* and *S. oneilli* on both Amazonian and Pacific versants, and I amplify knowledge of variation in all species. Scrocchi et al. (1993) provided a brief review of the southern South American species and literature subsequent to Peters (1960, 1965).

METHODS

General Methodology and Scale Terminology. This review is based on study of most specimens of *Sibynomorphus* from Ecuador and Peru in collections, including holotypes of all species except *S. petersi* and *S. vagus.* My own field experience with the genus is limited to a few specimens from northern Peru, here referred to *S. petersi.*

Systematic methods and characters used herein follow previous studies (e.g., Cadle, 1996, 2005; Cadle and Myers, 2003). I used the Dowling (1951) method for ventral counts (beginning the count with the first plate bordered on each side by the first dorsal row), but for most specimens, I also recorded preventral scales (unpaired plates anterior to the ventrals that are wider than long) for reasons detailed by Myers (1974: 37; 2003: 6–8). Scale terminology follows Peters (1960), but amplification of the scoring of some scales is useful.

Scales on the ventral surface of the head are highly variable in *Sibynomorphus* and other dipsadines. One or two pairs of infralabials are in contact posterior to the mental scale. Posterior to these contacting infralabials, I counted as *chin shields* those scales along the midline (no distinct mental groove in *Sibynomorphus*) that were about equal in length and width considering each scale individually. These scales are squarish or polygonal and occur in pairs with the occasional exception of a posterior shield that is unpaired (resulting in a chin shield count of 3.5 pairs, for example). Another one to three pairs of *gular* scales were often present posterior to the chin shields; gular scales are distinguished from the chin shields because each gular scale is wider than long. Gular scales were not scored for this study. The gular scales are followed by the unpaired preventrals (when present).

For the *Dipsas oreas* group (*D. oreas, D. elegans,* and *D. ellipsifera*) Cadle (2005: 71–73, fig. 1) described patterns of covariation between the shape of the loreal scale and whether the preocular was fused with the prefrontal or not. These scales are more uniform in species of *Sibynomorphus,* and a few specimens were intermediate between some of the six "loreal pattern" states defined by Cadle (2005). As in *Dipsas,* the loreal in *Sibynomorphus* was either squarish or polygonal, or much longer than tall, and the preocular was fused or not with the prefrontal. In addition, some specimens of *Sibynomorphus* have other patterns, such as multiple preoculars, which were not observed in the *D. oreas* group; these patterns are discussed in the species accounts.

Because of great variability in scutellation and color patterns in *Sibynomorphus,* I present detailed discussion of individual specimens where pertinent to facilitate future work on *Sibynomorphus.* For testing sexual dimorphism in ventral and subcaudal counts and color pattern characteristics, I used Student's *t* test on the sample means after testing for homogeneity of variances (Sokal and Rohlf, 1981). When variances were unequal (only in the case of color pattern characters for *Sibynomorphus petersi*), I used an approximation to the *t* test for two samples described by Sokal and Rohlf (1981: 408–412). Sexual dimorphism was also evident in relative tail lengths. However, because relative tail lengths are ratios (tail length/total length), the assumptions of the *t* test are unlikely to be met without tranforming the data, a process not undertaken here. However, the frequency distributions of relative tail lengths between the sexes of species of *Sibynomorphus* considered herein overlapped minimally or not at all.

Snout–vent lengths (SVLs) and total

lengths were measured with a meter stick or a plastic ruler to the nearest millimeter. For a few comparisons, I used head dimensions, which were measured with dial vernier calipers to the nearest 0.05 millimeter. Head lengths were measured in two ways: (1) obliquely from the tip of the snout to the posterior tip of the mandible (HL–mandible) and (2) from the tip of the snout to the posterior end of the interparietal suture (HL–parietal). Eye diameter (ED) was measured with dial vernier calipers under a dissecting microscope as the greatest horizontal dimension of the eye. Figure 3 was drawn with a camera lucida mounted in a dissecting microscope.

Hemipenial Techniques and Descriptions. Everted hemipenes of *Sibynomorphus petersi* and *S. williamsi* described herein are from field-everted organs. Hemipenes of *S. oligozonatus, S. vagrans,* and *S. vagus* were manually everted from the inverted organs of museum specimens according to methods detailed by Myers and Cadle (2003). Hemipenial terminology follows Myers (1974: 30–33), Myers and Campbell (1981), and Zaher (1999). Some remarks about the terminology of general orientation is useful because of some differences in the way inverted and everted organs are described. The position of inverted hemipenes is fixed relative to the snake's body and they can be described by standard anatomical terminology (e.g., dorsal/ventral, medial/lateral, proximal/distal) for orientation with reference to the snake's body. In addition, the number of subcaudal scales subtending portions of the inverted hemipenis is commonly used as a relative measure of proportions for inverted hemipenes.

On the other hand, everted hemipenes are frequently described once they have been separated from the snake's body and subjected to further preparation—eversion in the case of manual eversions, inflation, injection with colored jelly, etc. (Myers and Cadle, 2003). In descriptions of everted organs, structures on the hemipenis itself provide the best markers for orientation. The sulcus spermaticus provides a convenient landmark and the terms *sulcate* (side with the sulcus) and *asulcate* (side opposite the sulcus) were defined by Myers and Trueb (1967) to denote these surfaces of the hemipenial body. In *Sibynomorphus* and many other snakes the hemipenial body bears a nude pocket approximately midway between the sulcate and asulcate surfaces, a position referred to as *lateral* (e.g., Cadle, 2005; Cadle and Myers, 2003; and herein).[5] In this context, *lateral* is used with respect to the orientation provided by the sulcate/asulcate sides of the hemipenial body only, and not with respect to the snake's body. A laterally positioned nude pocket thus has a sulcate lip or edge (toward the sulcate side) and an asulcate lip or edge (toward the asulcate side). Terms such as proximal (toward the base of the organ) and distal (toward the apex) are still useful in describing everted hemipenes because their meaning is the same with respect to both inverted or everted organs.

Localities and Geographical Data. Reference to the "Río Zaña Study Site" in the account for *Sibynomorphus petersi* refers to a locality in western Cajamarca Department that is better known herpetologically than other localities in northern Peru; see Cadle (2005: 70–71) for discussion and additional references. Elevations for my col-

[5] Current use of the terms *sulcate, asulcate,* and *lateral* differs from definitions in Dowling and Savage's (1960) classic work. Dowling and Savage used the terms *sulcate* and *asulcate* to refer to the two primary tissue layers of the hemipenis: the *sulcate layer* referred to the entire external surface of the everted organ, which bears the sulcus spermaticus on one side; the *asulcate layer* referred to the internal tissue layer of the everted organ (Dowling and Savage, 1960: 19 and pl. I). Dowling and Savage (1960: 21) used the term *lateral* to refer to what is now called the asulcate surface of the organ and *medial* for what is now referred to as the sulcate surface. Myers and Trueb (1967) redefined *sulcate* and *asulcate* to their current usage because those terms seem most useful and least confusing as descriptors for the gross topology of hemipenes (the usual mode of study), rather than as names of tissue layers that are best studied in histological section.

lecting localities were determined in the field with a Thommen© altimeter calibrated in meters, sometimes in conjunction with topographic maps. Coordinates and elevations for other localities, unless otherwise stated, were derived from Paynter (1993); Stephens and Traylor (1983); Peruvian departmental maps published by the Instituto Geográfico Militar (IGM; now the Instituto Geográfico Nacional), Lima; or online versions of the gazetteers of the U.S. Board on Geographic Names at the GEOnet© Names Server: http://earth-info.nga.mil/gns/html/index.html. Stiglich (1922) is indispensable in locating obscure Peruvian localities, such as small haciendas, and I have also found occasional use for the Global Gazetteer (version 2.1, 26 January 2006) at www.fallingrain.com/world. Bracketed data in the list of specimens examined are inferences not supplied with the original collections data. Museum abbreviations used in the text are identified at the beginning of the *Specimens Examined and Locality Records*.

Geographical discussions follow Simpson (1975) for the names of the principal chains of the Andes in northern Peru. There is little cause for confusion except that some references and atlases (e.g., Hopkins, 1997) more finely divide the nomenclature of some of the ranges. In particular, I follow Simpson (1975) in using the name "Cordillera Oriental" for all of the Andean ranges lying east of the inter-Andean portion of the Río Marañon. Other authors use that term for the relatively low ridges east of the Río Huallaga and designate the higher mountains between the Río Marañon and Río Huallaga as "Cordillera Central" (see Fig. 7 and Simpson, 1975: 276). As used herein, the Cordillera Blanca, Cordillera Negra, and Cordillera de Huancabamba are parts of the Cordillera Occidental.

Key to Species of *Sibynomorphus* in Ecuador and Peru

Because of the variability of color patterns and scale characters within *Sibynomorphus*, individual specimens must be identified by a combination of characters and with careful attention to sexual differences. The six northern species of *Sibynomorphus* are rare or absent in most collections, and accurately identified comparative material is generally unavailable. As a consequence, misidentification of museum specimens is frequent. The most common misidentifications of northern *Sibynomorphus* in collections that I surveyed involved *S. petersi*, *S. vagus*, and *S. oneilli* (which is not saying much because *S. oligozonatus* has been known only from the holotype and *S. vagrans* only from the type series; *S. williamsi* is seemingly absent from non-Peruvian collections). Ecuadorian specimens of *S. petersi* were commonly misidentified as *Dipsas variegata* (following Peters, 1960) or, in older collections, as *Dipsas oreas* (see Cadle, 2005; Cadle and Myers, 2003, for discussion), whereas Peruvian specimens of *S. petersi* and *S. oneilli* were commonly misidentified as the better known *S. vagus*.

A previous key to all species of *Sibynomorphus* (Scrocchi et al., 1993) was adequate on the basis of variation within species known at the time. However, *S. oligozonatus* and *S. oneilli* were known only from their holotypes, and this report documents additional variation within all species that was not available to Scrocchi et al. (1993). For example, in their key, color pattern characteristics (with or without definitive bands, number of dorsal bands) were critical to differentiating some species (*S. petersi*, *S. oneilli*, *S. vagus*), but on the basis of the new material examined for this report, I infer extremely variable color patterns within these species (e.g., "definitive bands" present in some individuals of *S. petersi* and *S. vagus* and individuals without bands in *S. oneilli*). Indeed, the variation of color patterns and scutellation within most of the northern species of *Sibynomorphus* and overlap of meristic characters between species made the construction of a workable key difficult. I have not studied species of *Sibynomorphus* that

occur south of the Amazon basin in any detail, but the following key should permit identification of species known from Peru and Ecuador. Considering present understanding of variation within these species and their geographic distributions, not to mention the possibility of new species occurring in this area, the key should be used in conjunction with detailed descriptions and comparisons of specimens when possible.

A few comments concerning the presence or absence of a separate preocular used in the first couplet of the key should be made. The key considers only the "normal" conditions of the preocular(s) in *Sibynomorphus*—that is, cases in which a single preocular superior to the loreal is present (Cadle 2005; Peters, 1960: 26; Figs. 11, 15, 23 herein), cases in which this preocular is fused with the prefrontal scale and a separate preocular is absent (see Fig. 3), or cases in which more than one preocular is present, in which case the loreal is separated from the eye by the inferior preocular(s). Less commonly, an irregular preocular can be formed by, for example, a suture across the posterior corner of the loreal. In the key, these irregular conditions would not be considered in determining presence or absence of a preocular.

That said, I should enter a caveat: the presence or absence of a separate preocular seems to be highly variable intraspecifically within some species of *Dipsas* (e.g., Cadle, 2005; Cadle and Myers, 2003). Although *Sibynomorphus* seems less variable in this character than *Dipsas*, some of the species in the key are represented by few specimens, and this character could prove more variable once sample sizes are larger. For this reason, use of the key in conjunction with the detailed discussions and illustrations in the species accounts will provide more accurate identifications.

To facilitate the identification of a specimen in hand, Table 1 provides summaries of systematic characters for all six species of *Sibynomorphus* occurring in Ecuador or Peru. The summary distributions in the key are documented herein.

KEY

1. Supralabials 6 or 7, with 3–4 or 4–5 touching the eye. No separate preocular (preocular fused with prefrontal). Venter usually only lightly spotted with dark pigment, if at all, or dusky and without discrete spots. Discrete crossbands on body present at least anteriorly, and anteriorly at least twice the width of the pale interspaces 2

   Supralabials 8 or more, with 4–5 touching the eye (rarely fewer than 8). One or more preoculars usually present (some individuals of *S. oneilli* lack separate preoculars). Venter usually heavily pigmented, often with half-moon–shaped or squarish spots. Distinct dorsal crossbands present or not, wider than interspaces or not 3

2. Distinct bold crossbands present only on anterior half of body, broken into series of paler vertebral and lateral blotches posteriorly; dorsal blotches on posterior body distinctly narrower than pale interspaces. Head only slightly broader than neck. Known variation in ventrals: 177 (one female), 145 (two males), and 163 (one male) ..... *Sibynomorphus oligozonatus* Orcés and Almendáriz
   (Andes of Azuay and Loja Provinces, southwestern Ecuador, Pacific versant; one specimen without specific locality from Piura Department, Peru)

   Distinct bold crossbands present the whole length of the body (often broken into middorsal and offset lateral blotches posteriorly, but these maintain their boldness); dorsal blotches on posterior body equivalent to, or (usually) slightly wider than, pale interspaces. Head distinctly broader than neck. Known variation in ventrals: 181–188 (females), 173–182 (males) ..... *Sibynomorphus williamsi* Carrillo de Espinoza
   (coastal lomas formations and Andean foothills and slopes in Lima and Ancash Departments, Peru)

3. Anterior body with 5–10 discrete crossbands that are much broader than the pale interspaces (bands encompass 5–9 dorsal rows middorsally, 3–6 rows laterally, excluding the nape band, which is always wider than any other bands; interspaces encompass 0.5–2 scale rows middorsally). Top of head very ornately patterned, including a relatively broad irregular dark band across the posterior edge of the prefrontals (sometimes interrupted at one or more points). Ventrals 149–155 in males,

154–159 in females. Subcaudals 80–87 in males, 72–79 in females ---------- *Sibynomorphus vagrans* Dunn (known only from the vicinity of Bellavista, Cajamarca Department, in the inter-Andean valley of the upper Río Marañón of northern Peru; Amazonian versant).

Discrete crossbands on anterior body present or not; if present anteriorly, bands are only slightly wider than, or equivalent to, the pale interspaces (usually narrower than interspaces). Top of head ornately patterned or not, but without a discrete band across the posterior edge of the prefrontals ---------- 4

4. Ventrals <155 (known range 144–152) in males, <160 (known range 151–158) in females. Subcaudals ≤65 in males, ≤60 in females. Maximum known size: 368 mm SVL (males), 326 mm SVL (females) ---------- *Sibynomorphus vagus* (Jan) (known only from the vicinity of Huancabamba, Piura Department, Peru; Amazonian versant)

Ventrals >150 in males, >160 in females. Subcaudals >60 in males, >55 in females. Maximum size to ≥470 mm SVL in males, ≥595 mm SVL in females ---------- 5

5. A discrete dark spot or irregular marking, usually outlined with a narrow pale edge, on each prefrontal; head generally with many dark markings. Dorsum usually with narrow, often zigzag, crossbands (bands may be reduced to an indistinct series of irregular vertebral and lateral spots). Infralabials usually 10–12 (rarely 9). Ventrals: males, 164–183; females, 173–188. Subcaudals: males, 75–87; females, 65–77 ---------- *Sibynomorphus petersi* Orcés and Almendáriz (Azuay and Loja Provinces, southwestern Ecuador, south along the western slope of the Cordillera Occidental to southern Ancash Department, Peru; Río Chotano valley, Amazonian versant, in Cajamarca Department, Peru)

No discrete dark spots outlined with a pale edge on prefrontals; top of head unpatterned or with a few dark markings, primarily on parietals and frontal. Discrete narrow blackish crossbands usually present the length of the body; anterior bands about equal to interspaces; posterior bands much narrower than interspaces (crossbands may be broken up on posterior body and some individuals lack bands, having instead an obscure network or reticulations). Infralabials 8 or 9. Ventrals: males, 152–168; females, 163–177. Subcaudals: males, 62–77; females, 56–64 ---------- *Sibynomorphus oneilli* Rossman and Thomas (Cordillera Oriental and Cordillera Occidental from southern Ancash to southern Cajamarca and Amazonas Departments, Peru, in the Río Marañón and Río Santa drainages)

Sibynomorphus oligozonatus Orcés and Almendáriz Figures 1–6

Dipsas mikanii oreas, part: Parker, 1938: 444 (a female from the "Catamayo valley 30 km west of Loja," here inferred to be BMNH 1935.11.3.108, which Parker thought possibly represented a "distinct species" from the rest of the series) (misidentification). The rest of this series discussed by Parker is identified here as *S. petersi.*

Sibynomorphus oligozonatus Orcés and Almendáriz (1989). Type locality: "Zhila (2,250 m) 79°17′26″W, 03°39′45″S [see footnote 19], parroquia Oña, cantón Girón, Provincia Azuay [Ecuador]." Holotype, EPN 3612 (Fig. 1). Almendáriz and Orcés (2004).

Notes on the Holotype of *Sibynomorphus oligozonatus*

With a few minor exceptions, my data for the holotype of *Sibynomorphus oligozonatus* (EPN 3612) are virtually identical to those reported in the original description (Orcés and Almendáriz, 1989) (see Table 2). The difference in ventral counts is probably due to different methods of counting (i.e., whether the preventrals were included in the ventral count or not—see *Methods*). My notes for the holotype indicate that the "tail tip is damaged and may include one or two additional subcaudals."

The holotype (Fig. 1) has broad dark brown crossbands on the anterior half of the body, alternating side to side. Posteriorly, these crossbands break up into narrow zigzag lateral bars alternating with an irregular series of middorsal blotches. The dorsal ground color (interspaces) is whitish anteriorly, medium brown posteriorly. The venter is immaculate white posterior to the head, with fine dark speckling displaced laterally and increasing posteriorly.

The only substantive difference between my assessment of the holotype and that in the original description concerns the maturity of the specimen. Orcés and

TABLE 1. SUMMARY OF STANDARD TAXONOMIC DATA FOR THE SIX SPECIES OF *SIBYNOMORPHUS* THAT OCCUR IN ECUADOR OR PERU. FOR HEAD SCALES, EACH SIDE OF THE HEAD OF EACH SPECIMEN WAS SCORED AS AN INDEPENDENT OBSERVATION BECAUSE OF FREQUENT ASYMMETRY. *N* = NUMBER OF SPECIMENS OR OBSERVATIONS. SVL = SNOUT-VENT LENGTH. MEANS ARE ±1 SD. FOR *S. OLIGOZONATUS*, ONLY CHARACTER RANGES ARE GIVEN BECAUSE OF SMALL SAMPLE SIZES (3 MALES, 1 FEMALE). ADDITIONAL DATA SUMMARIES BY SPECIMEN OR GEOGRAPHY ARE GIVEN IN THE ACCOUNTS FOR *S. OLIGOZONATUS*, *S. ONEILLI*, AND *S. PETERSI*.

	Sibynomorphus sp.					
	oligozonatus	*oneilli*	*petersi*	*vagrans*	*vagus*	*williamsi*
Total length (SVL) (mm)						
Largest male	462 (348)	623 (470)	763 (609)[1]	543 (387)	483 (368)	563 (435)
Largest female	550 (428)	790 (624)	771 (595)	557 (425)	408 (326)	718 (561)
Tail length/total length						
Male	0.24–0.26	0.22–0.26 0.24 ± 0.014 (*N* = 9)	0.22–0.28 0.25 ± 0.02 (*N* = 8)	0.25–0.29 0.27 ± 0.01 (*N* = 13)	0.23–0.24 0.24 ± 0.005 (*N* = 4)	0.21–0.24 0.23 ± 0.01 (*N* = 5)
Female	0.22	0.20–0.22 0.21 ± 0.008 (*N* = 5)	0.20–0.24 0.22 ± 0.01 (*N* = 11)	0.23–0.26 0.24 ± 0.01 (*N* = 6)	0.20–0.21 0.20 ± 0.005 (*N* = 4)	0.19–0.22 0.20 ± 0.01 (*N* = 12)
Maxillary teeth	12 (*N* = 2) 13 (*N* = 1) 15 (*N* = 1)	13 (*N* = 5) 14 (*N* = 2) 15 (*N* = 4) 16 (*N* = 2)	14 (*N* = 3) 15 (*N* = 4) 16 (*N* = 2) 17 (*N* = 1)	15 (*N* = 2) 16 (*N* = 5) 17 (*N* = 2)	14 (*N* = 1) 15 (*N* = 2) 16 (*N* = 2)	12 (*N* = 2) 13 (*N* = 3) 14 (*N* = 1)
Dorsal scales	15–15–15	15–15–15 (*N* = 16) 15–15–13 (*N* = 1)	15–15–15	15–15–15	15–15–15	15–15–15
Ventrals						
Male	145 (*N* = 2), 163 (*N* = 1)	152–168 161.1 ± 5.22 (*N* = 10)	164–183 173.5 ± 5.39 (*N* = 11)	149–155 151.4 ± 1.66 (*N* = 13)	144–152 148.6 ± 3.44 (*N* = 5)	173–182 177.0 ± 3.61 (*N* = 5)
Female	177	163–173 167.0 ± 3.51 (*N* = 7)	173–188 178.5 ± 4.33 (*N* = 13)	154–159 157.0 ± 1.79 (*N* = 6)	151–158 154.0 ± 2.92 (*N* = 5)	181–188 184.0 ± 2.36 (*N* = 10)
Subcaudals						
Male	66–68	62–77 67.7 ± 5.07 (*N* = 9)	75–87 81.0 ± 3.66 (*N* = 8)	80–87[2] 83.4 ± 2.43 (*N* = 13)	60–65 62.8 ± 2.22 (*N* = 4)	67–73 69.0 ± 2.55 (*N* = 5)
Female	68	57–64 61.0 ± 2.65 (*N* = 5)	65–77 73.0 ± 3.69 (*N* = 12)	72–79 73.8 ± 2.64 (*N* = 6)	56–60 57.2 ± 1.89 (*N* = 4)	56–66 61.6 ± 3.28 (*N* = 9)

TABLE 1. CONTINUED.

	Sibynomorphus sp.					
	oligozonatus	*oneilli*	*petersi*	*vagrans*	*vagus*	*williamsi*
Anal scale	Single	Single	Single	Single	Single	Single
Preoculars	0 (N = 8)	0 (N = 11) 1 (N = 17) 2 (N = 2) 3 (N = 2)	1 (N = 35) 2 (N = 6) 3 (N = 3)	1 (N = 26) 2 (N = 12)	1 (N = 20)	0 (N = 32)
Postoculars	2 (N = 6) 3 (N = 2)	2 (N = 29) 3 (N = 1)	2 (N = 46) 3 (N = 1)	2 (N = 35) 3 (N = 3)	1 (N = 1) 2 (N = 19)	2 (N = 24) 3 (N = 4)
Primary temporals	2 (N = 8)	1 (N = 5) 2 (N = 31)	1 (N = 6) 2 (N = 39)	1 (N = 8) 2 (N = 25) 3 (N = 5)	1 (N = 19) 2 (N = 1)	2 (N = 23) 3 (N = 6)
Secondary temporals	3 (N = 7) 4 (N = 1)	1 (N = 1) 2 (N = 3) 3 (N = 21) 4 (N = 5)	2 (N = 6) 3 (N = 38) 4 (N = 2)	2 (N = 15) 3 (N = 23)	2 (N = 18) 3 (N = 2)	2 (N = 1) 3 (N = 21) 4 (N = 7)
Tertiary temporals	3 (N = 4)[3]	2 (N = 2) 3 (N = 9) 4 (N = 15)	2 (N = 2)[3] 3 (N = 4) 4 (N = 2)	3 (N = 33) 4 (N = 5)	0 (N = 1) 1 (N = 1) 2 (N = 13) 3 (N = 5)	3 (N = 13) 4 (N = 15) 5 (N = 1)
Supralabials (touching eye)	6 (3–4) N = 4 7 (3–4) N = 1 7 (4–5) N = 2	6 (3–4) N = 2 7 (3–4) N = 8 8 (3–5) N = 4 8 (4–5) N = 17 8 (4–6) N = 1 9 (4–6) N = 1 10 (4–6) N = 1	7 (3–4) N = 2 7 (4–5) N = 2 8 (4–5) N = 35 9 (4–5) N = 2	8 (3–5) (N = 1) 8 (4–5) (N = 33) 9 (4–5) (N = 1) 9 (4–6) (N = 1) 10 (4–6) (N = 2)	7 (3–4) N = 3 7 (4–5) N = 4 8 (3–4) N = 2 8 (4–5) N = 11	6 (3–4) (N = 29) 7 (3–4) (N = 1)
Infralabials	9 (N = 1) 10 (N = 5)	8 (N = 1) 9 (N = 3) 10 (N = 9) 11 (N = 16) 12 (N = 3) 13 (N = 1)	9 (N = 5) 10 (N = 22) 11 (N = 10) 12 (N = 4)	9 (N = 1) 10 (N = 4) 11 (N = 19) 12 (N = 12) 13 (N = 2)	8 N = 2 9 N = 8 10 N = 9 11 N = 1	8 (N = 1) 9 (N = 4) 10 (N = 20) 11 (N = 3)

TABLE 1. CONTINUED

	Sibynomorphus sp.					
	oligozonatus	*oneilli*	*petersi*	*vagrans*	*vagus*	*williamsi*
Number of dorsal bands or blotches on body	(Generally only anterior body with well-defined bands)	38–63 when present; sometimes absent or fragmented	Male: 29–35 31.2 ± 1.69 (*N* = 10) Female: 31–59 38.0 ± 8.01 (*N* = 12) (bands sometimes absent)	(Only anterior body with well-defined bands)	(Often irregular flecks or reticulations; bands, when present, are discrete only anteriorly)	35–48 41.5 ± 3.74 (*N* = 15)

[1] The largest male is the holotype (Orcés and Almendáriz, 1989), which was not examined in this study. The largest male examined by me was 657+ mm total length, 520 mm SVL. On the basis of measurements in the original description, the holotype has a shorter tail (20% of total length) than males I examined.

[2] Peters (1960) reported a lower bound of 74 subcaudals for male *S. vagrans*, which could be a count obtained from one of the paratypes not examined for this study (see text footnote 25).

[3] Extensively fragmented or fused tertiary temporals, making scoring somewhat arbitrary.

Almendáriz (1989) reported that the holotype of *Sibynomorphus oligozonatus* was an adult male. However, several characteristics indicate that it is more likely a subadult (the hemipenis of the holotype is described subsequently in this account). Cadle (1996: 43–44), following a suggestion of Charles W. Myers, reviewed observations indicating that the extent of mineralization of hemipenial spines could be used to infer the sexual maturity of colubrids. Immature male snakes have nonmineralized hemipenial spines and spinules, whereas in adults, these ornaments are mineralized, a characteristic that can be assessed with a fine needle (some experience and comparisons of juveniles and adults is helpful);[6] the mineralization of spines in adult hemipenes compared with juveniles was also noted by Cope (1895: 189). A specific pattern of progressive mineralization of individual spines (tip to base) and on the hemipenis overall (proximal to distal) is apparent.

The proximal edge of the capitulum of the hemipenis of the holotype of *S. oligozonatus* is fringed with nonmineralized or poorly mineralized spinules (rather than mineralized spines). In addition, spines on the hemipenial body proximal to the capitulum are mineralized only at their tips. These characteristics suggest that the specimen is not fully mature, and the holotype is also relatively small (SVL 265 mm, total length 351 mm) compared with the other referred males, AMNH 110587 (SVL 330 mm, total length 446 mm) and MUSM 2196 (SVL 348 mm, total length 462 mm). These characters are only suggestive that the holotype is not fully adult and more definitive internal examination

[6] If sufficient material, including juveniles to adults, is available, a useful technique for visualizing hemipenial spine mineralization is a simple adaptation of methods for clearing and alizarin staining to demonstrate mineralized tissue such as bone (e.g., Dingerkus and Uhler, 1977). Cadle (1996) used this approach to examine the ontogeny of spine mineralization in *Geodipsas*.

Table 2. Scale counts, measurements, and other data for specimens of *Sibynomorphus oligozonatus*. Bilateral counts are separated by a solidus (left/right). SVL = snout-vent length. Bracketed data for the holotype are from the original description (Orcés and Almendáriz, 1989) and are given only in cases of discrepancy from my own data (see text).

	EPN 3612 Holotype Subadult (?) male	AMNH 110587 Adult male	BMNH 1935.11.3.108 Adult female	MUSM 2192 Adult male
Total Length (SVL) (mm)	351 (265) [358 (273)]	446 (330)	550 (428)	462 (348)
Tail length (mm)	86 [85]	116	122	114
Tail length/total length	0.24	0.26	0.22	0.25
Maxillary teeth	12	13	12	15
Dorsal scales	15–15–15	15–15–15	15–15–15	15–15–15
Ventrals (+preventrals)	145 (+2) [148; preventrals not recorded]	145 (+1)	177 (+2)	163 (preventrals not recorded
Subcaudals	66 [67]	68	66	68
Anal scale	Single	Single	Single	Single
Preoculars (loreals)	0/0 (1/1)	0/0 (1/1)	0/0 (1/1)	0/0 (1/1)
Postoculars	2/2	2/2	3/3	2/2
Temporals				
Primary	2/2	2/2	2/2	2/2
Secondary	3/3	3/3	3/4	3/3
Tertiary	3/3	3/3	[fragmented]	?/?
Supralabials (touching eye)	6 (3 + 4)/6 (3 + 4)	7 (4 + 5)/7 (4 + 5)	6 (3 + 4)/7 (3 + 4)	6 (3 + 4)/? (3 + 4)
Infralabials	10/9 [10]	10/10	10/10	?/?

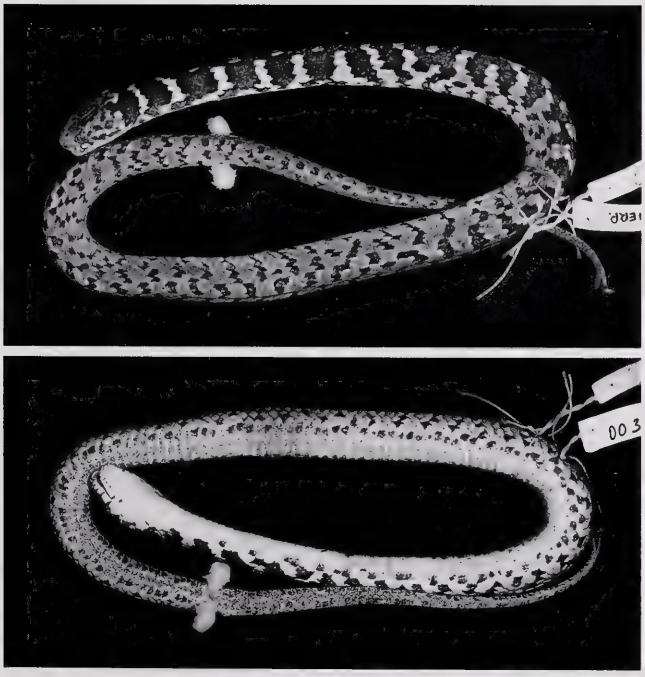


Figure 1. *Sibynomorphus oligozonatus*. Holotype in dorsal and ventral views (EPN 3612; Azuay Province, Ecuador). Subadult male, 265 mm SVL.

of reproductive organs was not undertaken.

New Material and Comparison of Specimens Referred to *Sibynomorphus oligozonatus*

Sibynomorphus oligozonatus has previously been known only from the holotype, EPN 3612. I refer three additional specimens to this taxon: AMNH 110587, BMNH 1935.11.3.108, and MUSM 2192. I was able to make side-by-side comparisons of BMNH 1935.11.3.108 and the holotype and subsequently made side-by-side comparisons of AMNH 110587 and BMNH 1935.11.3.108. Later I determined that MUSM 2192 should be referred to this species. Standard characteristics of each specimen are given in Table 2.

BMNH 1935.11.3.108 (Fig. 2) is an adult female from approximately 70 km SSW of the type locality. It was part of a collection from southern Ecuador obtained for the British Museum by Clodov-

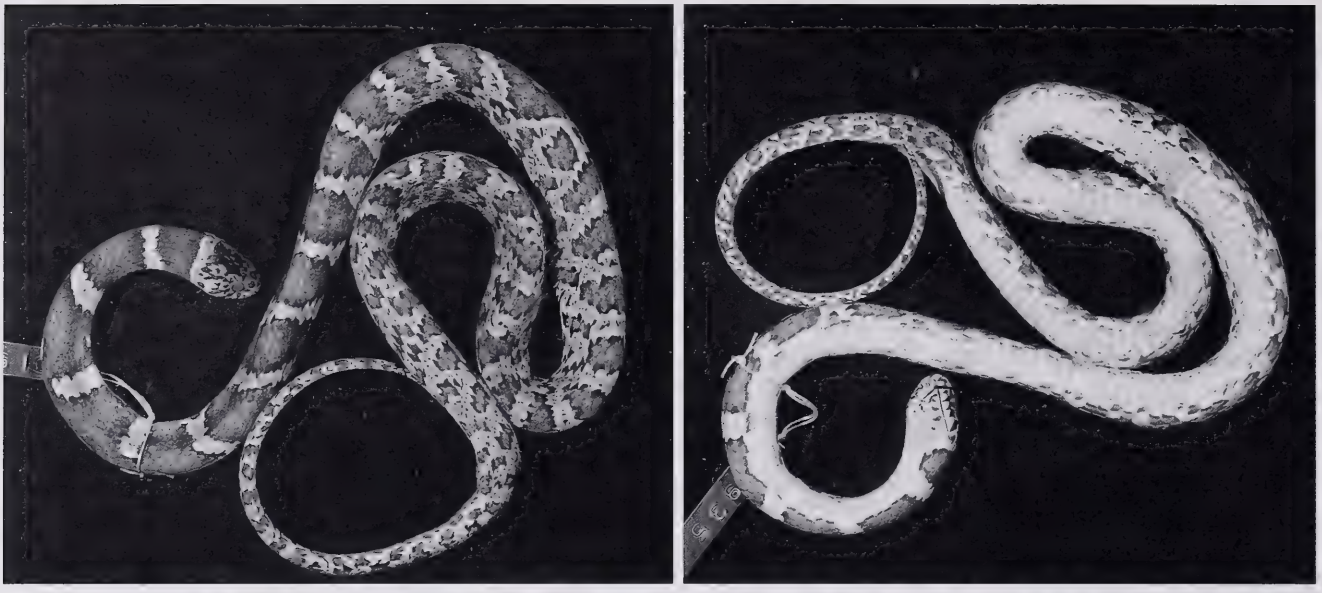


Figure 2. *Sibynomorphus oligozonatus*. Dorsal and ventral views of BMNH 1935.11.3.108 (Loja Province, Ecuador). Female, 428 mm SVL. The specimen illustrates the typical pattern in the known specimens: broad anterior dorsal crossbands, fragmented posterior bands, and relatively unpatterned venter.

eo Carrión (Parker, 1930a, 1930b, 1932, 1934, 1938). Parker (1938) referred several specimens in this collection to "*Dipsas mikanii oreas*" (= *Dipsas oreas*; Cadle, 2005). Rather peculiarly for a moderately sized collection from this region, none of the snakes that Parker referred to *D. oreas* appear to represent that species. Instead, they comprise the single specimen here identified as *Sibynomorphus oligozonatus* and a larger series I identify as *S. petersi* (see subsequent species account).[7] Parker (1938: 444) did not use BMNH collection numbers, but he noted that one of the females "differs from other specimens in having a smaller eye, a higher and narrower rostral, and the first labial in contact with the loreal; it may possibly represent a distinct species." BMNH 1935.11.3.108 matches the locality and characteristics given by Parker, including ventral and subcaudal counts that are virtually identical to mine.

AMNH 110587 is an adult male roadkilled specimen collected by Charles W. Myers on 12 February 1974 approximately 25 km northwest of the type locality. MUSM 2192 is an adult male from "Piura, Peru" (department or city not specified, here assumed to refer to the department) collected by Otavio Ruíz with no additional data. MUSM 2192 is soft and in poor condition; its scale counts were determined only with difficulty. (Another specimen possibly referable to *S. oligozonatus*, MUSM 2248, with locality "Piura" but no collector or date, is very soft and deteriorated. Its color pattern was apparently similar to MUSM 2192 but its condition precluded accurate scale counts, etc. It will not be considered further here.)

Because so few specimens of *Sibynomorphus oligozonatus* are known and they exhibit some differences in scutellation and color pattern, I herewith highlight features suggesting that these are conspecific and note some differences among them. Nonetheless, some characteristics of the

[7] Although *Dipsas oreas* is known from the same region as Carrión's collections (Cadle, 2005), the presence of *Sibynomorphus* in his collection and the apparent absence of *D. oreas* suggest that his collections were from drier, more open habitats (as opposed to humid forested habitats). *Dipsas oreas* is restricted to humid forests (Cadle, 2005), whereas species of *Sibynomorphus* in Ecuador and Peru generally occur in subhumid to arid environments, such as dry deciduous forests or thorn forests, which predominate in this region.

specimens make the interpretation of differences somewhat difficult with so few specimens. For example, the holotype is a subadult male and smaller than the other males, AMNH 110587 and MUSM 2192, whereas BMNH 1935.11.3.108 is a large female (Table 2). The head shape and body proportions of AMNH 110587 were difficult to assess because it is flattened, somewhat desiccated, and has a damaged head. More than likely there would be changes in shape associated with growth as well, rendering comparisons of shape characters (e.g., the distinctive head shape of BMNH 1935.11.3.108) between the small holotype and other specimens problematic. Similarly, MUSM 2192 is soft, in poor condition, and has a damaged head. These factors made it difficult to assess the relative contributions of size, sexual dimorphism, and other sources of variation.

Scutellation and Body Proportions. Two of the males, AMNH 110587 and the holotype, are nearly identical in scutellation (Table 2). Especially significant are the very low ventral counts, approached only by a few specimens of *Sibynomorphus vagrans* among the other species of Ecuador or Peru (male *S. vagrans* have many more subcaudals than either AMNH 110587 or EPN 3612). On the other hand, MUSM 2192 has considerably more ventrals than either of the other two males.

In contrast, the female, BMNH 1935.11.3.108, has considerably more ventrals than two of the males (EPN 3612, AMNH 110587; Table 2). The difference is probably accounted for by sexual dimorphism and perhaps geographic variation, but the disparity in ventral counts (32) is greater than has been reported for males and females of any other species of *Sibynomorphus* (see later comparisons herein; Scrocchi et al. 1993). The closest approach to this difference among the northern species of *Sibynomorphus* is in *S. petersi,* in which the minimum and maximum ventral counts (male and female, respectively) differ by 24.

Other differences among the three specimens are found in the configuration of scales in the loreal region. In AMNH 110587 supralabials 2–4 touch the loreal scale (the first supralabial is well separated from the loreal by the posterior nasal scale), whereas supralabials 1–3 border the loreal in BMNH 1935.11.3.108 (Fig. 3); in MUSM 2192 supralabials 2–3 broadly contact the loreal but on each side, the first supralabial also touches the loreal at a point. In the holotype, supralabials 2–3 border the loreal. In the AMNH specimen, supralabials 4 and 5 border the eye, whereas supralabials 3 and 4 border the eye in the other specimens. Scales in the loreal region vary substantially within some other Dipsadini (Cadle, 2005: 71–73; Peters, 1960: 25), and the variations among the referred specimens of *Sibynomorphus oligozonatus* do not seem extreme. The differences among the specimens in the relationships of the supralabials, loreal, and eye could reflect slightly different head shapes or proportions (see below). Differences among these specimens in other scutellation characters (Table 2) are typical of those observed in other Dipsadini.

BMNH 1935.11.3.108 has one unusual character of the dorsal head plates. Each supraocular is divided by a suture extending from the posterolateral angles of the frontal to the dorsal midpoint of the eye (Fig. 3). These sutures are very regular, well formed, and bilaterally symmetrical (i.e., each supraocular is identically divided). I am not aware of other colubrids with this variation, although Peters (1960: 25) reported fusions among some of the dorsal head plates (e.g., internasals, prefrontals) within *Dipsas.* BMNH 1935.11.3.108 also has more irregular scales in the temporal region than either AMNH 110587 or EPN 3612, but irregularities in this region are characteristic of many species of Dipsadini.

The three specimens differ somewhat in general body form and head shape, but the size differences among specimens and the general conditions of AMNH 110587 and

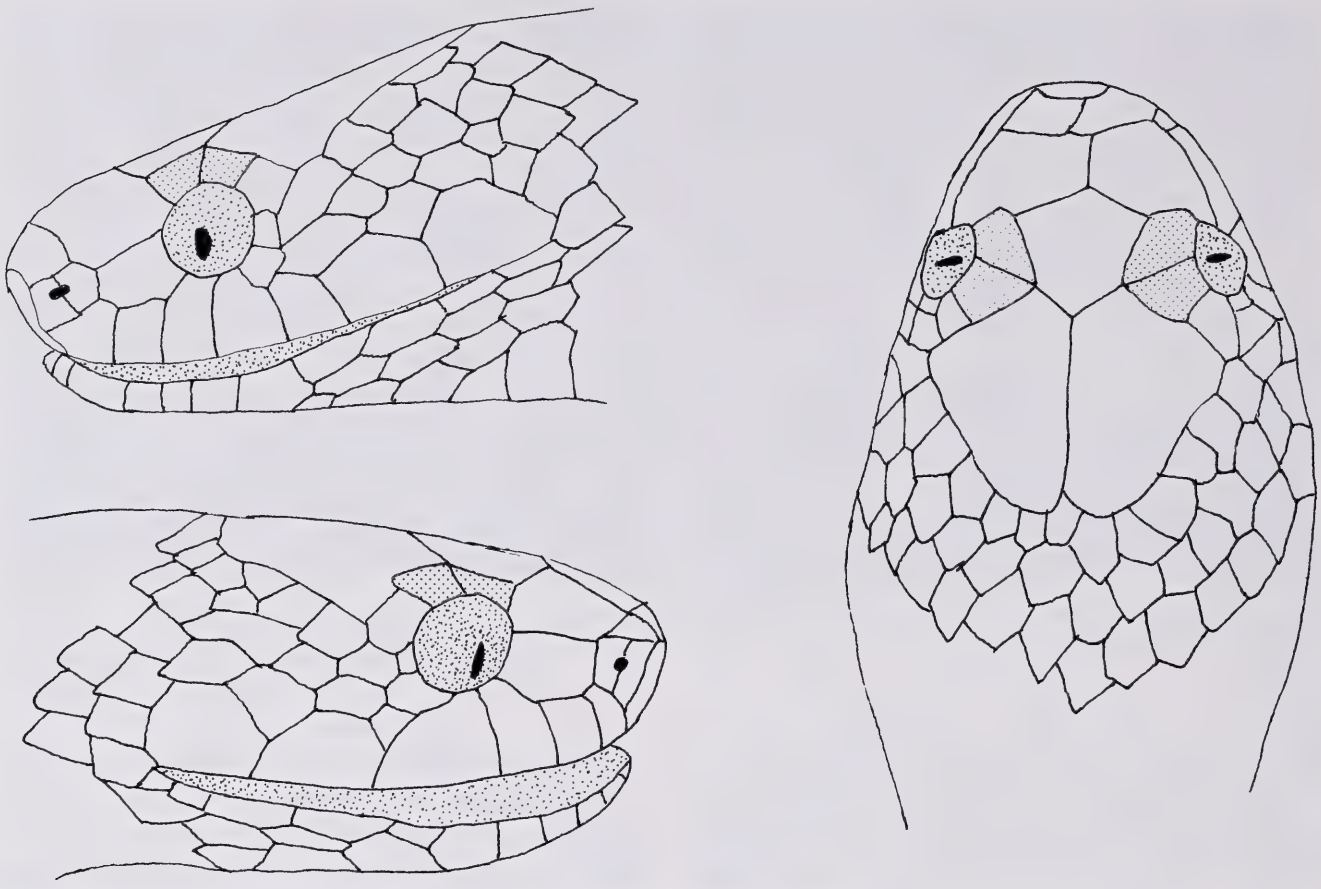


Figure 3. Head scales of *Sibynomorphus oligozonatus* (BMNH 1935.11.3.108) in left and right lateral views and in dorsal view. The lateral views indicate the blunt, short appearance of the snout (see also Fig. 4). The peculiar divided supraocular scales (shaded dorsal head plates) are unique to this specimen.

MUSM 2192 make these comparisons problematic. Judging from BMNH 1935.11.3.108, adult *Sibynomorphus oligozonatus* have a peculiarly foreshortened and very blunt snout (Fig. 4). It is not possible to judge precisely the physiognomy of AMNH 110587, especially the head, because it has been flattened. It seems to have a somewhat longer and more acuminate snout than BMNH 1935.11.3.108, but this could be entirely due to artificial deformation. The head shapes of BMNH 1935.11.3.108 and EPN 3612 are similar; the head of MUSM 2192 is damaged but appears to be particularly blunt.

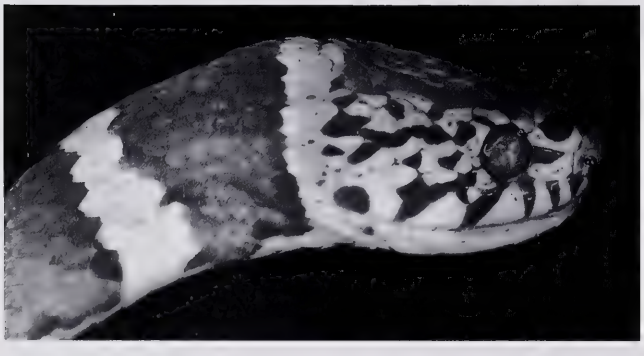


Figure 4. *Sibynomorphus oligozonatus.* Lateral view of head, BMNH 1935.11.3.108.

Some differences in head size seem apparent between the adult specimens of *Sibynomorphus oligozonatus,* AMNH 110587 (male), BMNH 1935.11.3.108 (female), and MUSM 2192 (male), even accounting for distortion brought about by damage to the AMNH specimen. AMNH 110587 has a larger head in relation to SVL (4.0% or 3.7% by HL–mandible and HL–interparietal, respectively) than the BMNH specimen (3.5% and 2.6%, respectively) or MUSM 2192 (3.0% by HL–interparietal; lower jaws are damaged, precluding accurate measurement of HL–mandible). Sexual dimorphism in head length relative to SVL is widespread in

snakes—for example, in nearly half of the species and 43% of the genera in one taxonomically diverse survey (Shine, 1991). However, Shine (1991) found that female snakes commonly had relatively larger heads in most genera (40 of 61 genera, omitting taxa without dimorphism). Thus, if the difference in head proportions between the males and female *S. oligozonatus* truly represents sexual dimorphism, it is of a relatively less common pattern among snakes.

Color Patterns. The color patterns of specimens referred to *Sibynomorphus oligozonatus* are similar (Figs. 1, 2, 5, 6). Dorsally, all specimens have broad anterior crossbands that begin to fragment at about one-third to one-half the body length. After the point of fragmentation, a series of middorsal blotches or saddles tends to alternate with lateral vertical bars or blotches. In BMNH 1935.11.3.108 and MUSM 2192, the middorsal blotches and the lateral bars are larger and more regular than in the holotype or in AMNH 110587; the BMNH and MUSM specimens have more complete crossbands than either of the other specimens. The crossbands of all specimens end on the outer one-quarter of the ventral plates.

In three specimens, there is a tendency, more pronounced in EPN 3612 and AMNH 110587 than in BMNH 1935.11.3.108 or MUSM 2192, for the anterior crossbands to be offset (i.e., corresponding portions of the bands on either side are displaced middorsally). In the BMNH specimen, crossbands 3–5 are offset, whereas in EPN 3612 and AMNH 110587, all anterior crossbands except the first one or two are offset. None of the complete crossbands in MUSM 2196 are offset. In AMNH 110587, BMNH 1935.11.3.108, and MUSM 2196, the central parts of the crossbands tend to be somewhat lighter than peripheral parts (i.e., bands appear dark-edged); this character was not recorded for the holotype.

The venter of all specimens has narrow irregular rectangles of dark pigment encroaching from the dorsum onto the edges of the ventral plates. Central parts of the ventral plates are speckled and flecked with tiny dark specks, which is much heavier in EPN 3612 and AMNH 110587, less so in BMNH 1935.11.3.108, and least in MUSM 2192. Pigmentation becomes denser on the posterior venter in all specimens, but to a lesser extent in BMNH 1935.11.3.108 and MUSM 2192 than in the others. Thus, BMNH 1935.11.3.108 and MUSM 2196 have relatively unmarked venters compared with the holotype and AMNH 110587.

The top of the head in BMNH 1935.11.3.108 is pale yellowish brown with bold black irregular marks all over. Supra- and infralabials in this specimen are pale yellowish with black suture lines (Fig. 4). The dorsal head pattern of the holotype is similar to BMNH 1935.11.3.108, including a pair of irregular bold longitudinal streaks posteriorly and a bold spot on each prefrontal scale. In AMNH 110587, the top of the head is grayish brown to medium brown without bold markings, except for an irregular spot on the anterior end of each parietal. Its markings are generally smaller and less distinct than in the holotype or BMNH specimen. Some suture lines on the supralabials and infralabials in AMNH 110587 are grayish brown, and some other grayish brown stippling is present on the supralabials, but they are not boldly marked as in the holotype or the BMNH specimen. In general, the dark markings on the heads of EPN 3612 and BMNH 1935.11.3.108 are distinctly blackish, whereas those in AMNH 110587 are grayish brown. MUSM 2192 has irregular spotting on top of the head, including a large spot at the anterior end of each parietal.

For several reasons, the identification of MUSM 2192 as *Sibynomorphus oligozonatus* is the most problematic of the four specimens. Its ventral count is much higher (163) than that of either of the other males (145), which brings it closer to the range of ventral counts in male *S. williamsi*

(173–182) (MUSM 2192 was previously identified in the MUSM catalogues as *S. williamsi*). These two species are otherwise very similar in scutellation (Table 1). The imprecise locality for MUSM 2192, "Piura" [Department], is intermediate between the other nearest localities for *S. oligozonatus* (Catamayo Valley of Loja Province, Ecuador) and *S. williamsi* (southern Ancash Department, Peru; see Fig. 43), although it is closer to the former.

Details of the banding pattern in MUSM 2192 compared with the other referred specimens of *S. oligozonatus* and *S. williamsi* convincingly demonstrate that MUSM 2192 should be referred to *S. oligozonatus*. These similarities to *S. oligozonatus* include (contrasting state for *S. williamsi* in parentheses; see Figs. 40–42) (1) abrupt transition from regular dorsal crossbands anteriorly to fragmented crossbands posteriorly (transition is gradual); (2) a narrow pale collar just behind the head, with the dark pigment of the first crossband not encroaching onto the head (pigment of first dark crossband extends up onto the head); (3) crossbands with distinctly darkened edges (bands lack distinctly darker edges); (4) crossbands brown (bands usually distinctly blackish in preservative, although this could be because of preservation or storage); (5) posterior crossbands usually distinctly narrower than interspaces (posterior crossbands as wide as, or wider, than interspaces); and (6) venter relatively immaculate (venter often, but not universally, dusky or with a ladder-like dark pattern or with dark spots posteriorly). Although the head shape of MUSM 2192 is difficult to assess because it is damaged, it seems to be relatively small and foreshortened, as in *S. oligozonatus*, compared with the longer, more acuminate head in *S. williamsi*.

Considering the highly variable coloration and scutellation in some other species of *Sibynomorphus*, the differences among the four specimens I refer to *S. oligozonatus* do not seem extreme, although the disparity in ventral counts (Table 2) between MUSM 2192 and the other males and between the female (BMNH 1935.11.3.108) and two of the males (EPN 3612, AMNH 110587) are remarkable. These specimens should be re-evaluated as additional material of this species accumulates. The following account is based on the collective characteristics of these four specimens.

Diagnosis

Sibynomorphus oligozonatus is a gray to grayish brown snake with broad dark crossbands anteriorly (narrowing and becoming broken into dorsal and lateral blotches posteriorly). Anterior crossbands are much broader than the interspaces and have regular, vertical edges and sometimes are offset. Posterior crossbands are usually much narrower than the interspaces. The venter is unmarked or has irregular dark speckling or spotting concentrated posteriorly. The head is foreshortened and blunt. The species has a low number of supralabials (6 or 7) and maxillary teeth (12–15). Males of *S. oligozonatus* have a low number of ventrals (145 in two males, 163 in another) and relatively long tail (24–26% of total length); these characters in the single known female (177 and 22%, respectively), are typical of some other species of *Sibynomorphus* (see Table 1).

Scrocchi et al. (1993) questioned whether *Sibynomorphus oligozonatus* was diagnosable from *S. vagrans* on the basis of the characters given in the original description. However, these two species differ in head shape and proportions, as well as several scale characters. *Sibynomorphus oligozonatus* has a short head and blunt snout (Fig. 4), lacks preoculars in the known specimens (i.e., the preocular is fused with the prefrontal and only a loreal is present between the eye and posterior nasal), and has six or seven supralabials and fewer than 70 subcaudals. *Sibynomorphus vagrans* has a more elongate head and more pointed snout (compare Fig. 4 with Figs. 30, 31), has a preocular in addition to a loreal (occasionally 2 preoculars

and a loreal), and has eight to 10 supralabials and more than 70 subcaudals (Table 1).

Sibynomorphus oligozonatus differs in color pattern from *S. oneilli* (see Figs. 8–10). Both species have dark crossbands that are broader anteriorly than posteriorly (some *S. oneilli* lack bands; see following species account). In *S. oligozonatus,* the anterior crossbands are twice or more as broad as the pale interspaces, whereas on the anterior body in *S. oneilli,* the interspaces are about as broad as, or broader than, the dark crossbands. *Sibynomorphus oneilli* has a bold pattern of dark markings in an irregular checkerboard pattern or paired spots on each ventral plate, whereas the venter of *S. oligozonatus* is relatively unmarked (AMNH 110587 does have irregular dark speckling all over the venter and some larger spots that tend to be concentrated laterally, but this pattern does not resemble the heavily spotted venter of *S. oneilli*; see Figs. 9, 10, 12).

Sibynomorphus petersi occasionally has relatively broad anterior crossbands reminiscent of, but less regular than, those of *S. oligozonatus. Sibynomorphus petersi* has a preocular above the loreal (preocular absent in *S. oligozonatus*) and usually has eight supralabials (six or seven in *S. oligozonatus*). In addition, male *S. petersi* have more ventrals (164–183) than *S. oligozonatus. Sibynomorphus petersi* generally has a strongly patterned venter (Fig. 13 and following) compared with the relatively less patterned venter of *S. oligozonatus.*

Sibynomorphus oligozonatus differs from *S. vagus* in color pattern: broad anterior crossbands having regular, more or less vertical borders in *S. oligozonatus* versus either nonbanded (a vague network or fine reticulations) or with narrow, poorly formed, and irregular crossbands in *S. vagus. Sibynomorphus vagus* has fewer ventrals in females, has a preocular scale, usually has a single primary temporal, and has seven or eight supralabials.

Sibynomorphus oligozonatus differs from *S. williamsi* in having fewer ventrals (males: 145–163 vs. 173–182; females: 177 vs. 181–188), in head shape (*oligozonatus*: head slightly broader than neck, short and blunt; *williamsi*: head broader than neck, longer and acuminate), and in some aspects of color pattern. In *S. williamsi,* the first dorsal crossband usually encroaches broadly onto the nuchal region (see Figs. 41, 42), whereas in *S. oligozonatus,* the first crossband is separated narrowly from the head by a distinct narrow pale collar (Fig. 4). The dorsal bands in *S. williamsi* are bold and distinct the whole length of the body and tail (even when fragmented into a dorsal and lateral series of blotches), whereas in *S. oligozonatus,* the anterior bands are much bolder than the posterior ones. In *S. oligozonatus* the dorsal blotches on the posterior body are slightly to much narrower than the pale interspaces; the posterior dorsal blotches in *S. williamsi* are equivalent to or wider than the pale interspaces.

The color pattern of the BMNH and AMNH specimens of *Sibynomorphus oligozonatus* is reminiscent of some specimens of *Dipsas oreas,* which perhaps led Parker (1938) to refer the BMNH specimen to that species (as "*Dipsas mikanii oreas*"). However, *D. oreas* usually has a pair of large oval dark irregular spots on the dorsoposterior portion (primarily parietal scales) of the head (Cadle, 2005: 101–108), a strongly compressed body, and a relatively much larger eye (compare Fig. 4 with Cadle, 2005, fig. 21). The relative eye diameter of the BMNH specimen of *S. oligozonatus,* the only adult with an undamaged head, was 0.51% of SVL, whereas for 12 adult *D. oreas,* the eye averaged 0.73 ± 0.049% of SVL (range: 0.64–0.78%). Males of *S. oligozonatus* can be distinguished from *D. oreas* by having fewer ventrals (144–163 vs. 167–184 in *D. oreas*) and subcaudals (66–68 vs. 82–91 in *D. oreas*). The female referred to *S. oligozonatus* is similar to females of *D. oreas* except for a slightly lower subcaudal count (66 vs. 70–83) and the previously mentioned as-

pects of color pattern and body form. See Table 2 and Cadle (2005, table 1).

Description

Size and Scutellation. Tables 1 and 2 summarize taxonomic data for *Sibynomorphus oligozonatus.* Largest male 446 mm total length (330 mm SVL). Largest female 550 mm total length (428 mm SVL). Body somewhat compressed. Tail 24–26% of total length in three males, 22% in one female. Ventrals 145 (two males) to 163 (third known male), 177 in a female; ventrals preceded by one or two preventrals. Anal single. Subcaudals 66–68 in males, 66 in one female. Loreal and prefrontal bordering anterior edge of eye (no separate preocular) (Fig. 3); loreal longer than tall. Postoculars 2 or 3, primary temporals 2, secondary temporals 3 or 4, tertiary temporals (when discrete) 3. Supralabials most commonly 6 (3–4 bordering eye); other patterns 7 (3–4) or 7 (4–5). Infralabials 10 (9 on one side in the holotype). Chin shields in 2–3.5 pairs. Maxillary teeth 12–15 ($N = 4$).

As far as can be discerned with only four specimens, *Sibynomorphus oligozonatus* shows typical colubrid patterns of sexual dimorphism in size (female larger), ventral counts (female greater), and relative tail length (male longer). Despite the difference in relative tail length, subcaudal counts do not differ between the males and the female. Statistical tests were not performed on these comparisons because only four specimens are known.

Color in Life. Orcés and Almendáriz (1989) described the color of the holotype as follows (paraphrased): "Diffuse dark brown spots on the top and sides of the head. Dark brown bands on the anterior part of the body four scales wide, narrowing to one scale wide on the posterior body. Interspaces anteriorly pale brown, becoming grayish at midbody. Venter whitish, finely speckled with brown posteriorly." Charles W. Myers annotated his field catalog for AMNH 110587 with the comment "venter white," meaning simply that the venter lacked any wash colors such as yellow or orange, which are common on the venters of some colubrids (Charles W. Myers, personal communication); the venter of AMNH 110587 does have some dark spotting.

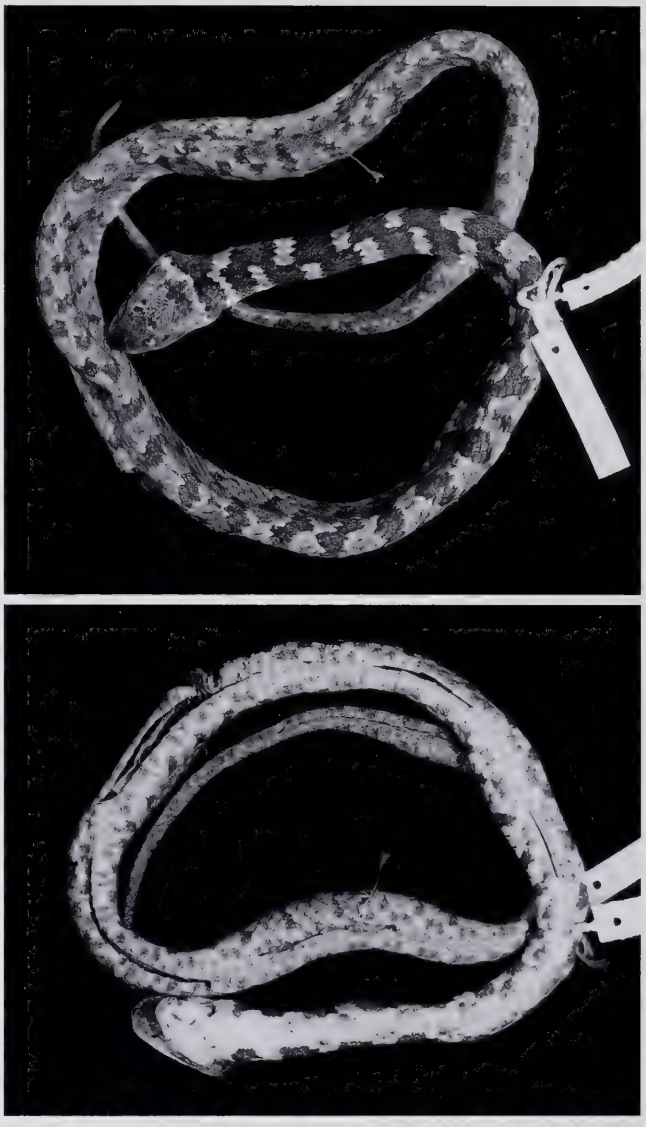


Figure 5. *Sibynomorphus oligozonatus.* Dorsal and ventral views of AMNH 110587 (Azuay Province, Ecuador). Male, 330 mm SVL.

Color in Preservative. The coloration of the four specimens in preservative is very similar (Figs. 1, 2, 5, 6). The dorsal pattern consists of broad anterior crossbands (4–10 dorsal rows wide) that progressively narrow posteriorly, fragmenting into middorsal and lateral blotches by about midbody. The crossbands are brown to blackish brown with a narrow darker border. In-

terspaces are gray, grayish white, or light (yellowish) brown. The top of the head is pale grayish or brown with bold dark spots and markings in an irregular pattern. The venter is pale gray without bold markings, but can have dark speckling that increases in density posteriorly. The color tones of the crossbands in MUSM 2192 are somewhat lighter brown (with reddish or chestnut tones) than the other specimens, but this could be preservation artifact (? light-induced fading). The coloration in preservative for three specimens is as follows (notes taken 2003 for AMNH 110587; 2004 for the others):

AMNH 110587 (Fig. 5): Dorsal ground color on anterior third of body grayish to grayish white, becoming grayish brown posteriorly. Approximately the anterior third of the body has bold blackish brown crossbands. The anterior five to six crossbands are offset middorsally, have vertical sides (i.e., they appear as squares or vertical rectangles viewed laterally), and tend to have somewhat paler centers than edges (central scales of the crossbands are mottled with dark brown and pale grayish brown, whereas peripheral scales are solid blackish brown). Anterior crossbands are four to five scales wide. Posteriorly the crossbands fragment abruptly into irregular middorsal and lateral blotches. The anterior dorsal crossbands encroach onto the outer quarter of the ventral plates. Dorsal scales in the interspaces between crossbands are finely flecked with minute dark brown specks. Interspaces anteriorly are 2–2.5 scale rows wide, increasing to 3 rows just before the point at which the dorsal crossbands fragment. Venter white, speckled, and irregularly spotted with dark brown, which increases posteriorly.

Top of the head brown (grayish brown on parietals), heavily flecked and spotted irregularly with dark brown. A single larger irregular spot is present at the anterior edge of each parietal. An indistinct narrow (two scales wide) pale grayish nape collar is behind the mouth commissure, followed by the first dorsal crossband.

BMNH 1935.11.3.108 (Figs. 2, 4): Dorsal ground color pale, somewhat yellowish, brown. Crossbands are medium brown with blackish edges <1 dorsal row wide. Under magnification their centers are flecked with minute pale specks, making their centers somewhat lighter than the edges. The first neck band is about 6 to 6.5 scale rows wide. The next two crossbands are 7 to 8 rows wide. Succeeding crossbands narrow to six, five, and four rows before breaking up into a series of dorsal saddles and lateral blotches or bars. All crossbands are complete middorsally and extend ventrally to the outer edges of the ventral plates. On the posterior body, the lateral blotches are very irregular in shape and poorly formed, whereas the dorsal saddles have a more regular shape. The venter is yellowish white with scattered dark markings, which become denser posteriorly and are mostly disposed on the lateral portions of the ventral plates.

Figure 6. *Sibynomorphus oligozonatus*. Dorsal and ventral views of MUSM 2192 from an unknown locality in Piura Department, Peru. Male, 348 mm SVL.

The top of head has bold, crisp (sharp edged) irregular blackish reticulations and spots in no distinct pattern. Supra- and infralabials are yellowish with bold black suture lines. Posterior to the region of bold head markings are a pair of scale rows relatively free of markings, forming a narrow pale nape collar; then follows the first crossband.

MUSM 2192 (Fig. 6): Dorsal crossbands are pale, somewhat reddish brown, each with a narrow (<1 dorsal scale row wide) dark brown border. Interspaces grayish. First neck crossband is 11 scale rows wide; then follow 11 to 12 discrete crossbands, progressively narrowing from 7–9 rows wide anteriorly to 4 rows wide posteriorly. Crossbands extend ventrally to the outer edges of the ventral scutes. Pale interspaces are 1.5–2 scale rows wide. The venter is immaculate grayish with a few small punctations on the edges of the plates. The top of the head is pale grayish brown with darker irregular spots (large spots on anterior edges of parietals and on other head scales). Supralabials have a few dark lines, but are generally pale. Infralabials and gular region are pale.

Etymology. The specific epithet, *oligozonatus*, comes from the Greek words *oli-*

go- (few) and *zona* (belt); the suffix *-atus* indicates possession. It refers to the "few transverse bands, much less numerous than is usual in the genus" (Orcés and Almendáriz, 1989: 63).

Hemipenis

The hemipenes of the holotype of *Sibynomorphus oligozonatus* are partially everted, and I first report details observable on them. Then follows a complete description of the everted organ of AMNH 110587. No differences were observed between the portions of these two organs that could be compared.

The hemipenis of the holotype (EPN 3612) is capitate and apparently slightly bilobed. The sulcus spermaticus divides within the capitulum, which is spinulate on the visible proximal portion; the spinules apparently correspond to the fringe of spines on the proximal edge of the capitulum of the everted organ of AMNH 110587 described below. These spinules in the holotype are nonmineralized or poorly mineralized. Proximal to the capitulum, the distal portion of the hemipenial body bears a battery of enlarged spines, which appear to be mineralized only at their tips. A nude pocket bordered on each side by a fleshy lobe is on the lateral side of the hemipenial body proximal to the abovementioned battery of spines.

The right hemipenis of AMNH 110587 was partially everted upon preservation. Full eversion was effected with the use of methods described by Myers and Cadle (2003). Although the organ is fully everted, it is not likely to be maximally expanded. Hence, the entire surface morphology of the hemipenis can be studied, but it is probably not as fully expanded as a fully everted fresh organ (see Myers and Cadle [2003] for discussion). In particular, the basal portion, which was everted before preservation, appears somewhat dehydrated and not fully expanded; a portion of the asulcate side of the capitulum also appears incompletely expanded.

Total length of the everted organ 15 mm, bilobed less than 1 mm. The relative proportions of the capitulum to base could not be assessed with accuracy because the base of the hemipenis is rather nonpliant and is probably not extended to its maximal state. The hemipenis is fully capitate and slightly bilobed. The capitulum is entirely calyculate and calyces are ornamented with fingerlike papillae; some of the more proximal papillae might have mineralized tips. A fringe of small mineralized spines encircles the proximal edge of the capitulum just distal to the overhang demarcating the capitulum; these spines are relatively straight and blunt. The calyces cover all aspects of the capitulum, including the crotch and medial portions of the lobes.

Proximal to the capitulum, a battery of enlarged hooked spines about three spines across encircles the entire organ. Proximal to the spinose midsection, the hemipenis bears scattered minute spinules, which appear to be denser toward the sulcate side of the organ. A very long nude pocket is positioned laterally on the organ and extends from the very base of the organ to the battery of spines. The pocket is bordered on each side by a prominent lobe. A single large hooked spine approximately twice the size of any other spines in the battery is present at the distal end of the sulcate edge of the nude pocket. At the level of the lobe on the asulcate edge of the pocket (i.e., the lip toward the asulcate side of the organ) are two large spines in a transverse row. Of these, the spine closest to the pocket is much larger than the one farther from the pocket, which is positioned nearly in the middle of the asulcate side (the lack of proper inflation of the base of the organ makes the position of this spine in a fully inflated organ difficult to ascertain). A gap ornamented with minute spinules separates these enlarged spines from the battery of spines around the midsection.

The sulcus spermaticus divides just within the capitulum. Its branches extend distally in centrolineal orientation, but ul-

timately pass to the outer (lateral) edges of each lobe. It is possible that the orientation of the branches could be somewhat different in a maximally expanded organ because of differential tissue expansion. The branches of the sulcus spermaticus end at the peripheral edge of the tip of each lobe (i.e., not continuing to the center of the lobe's apex).

Distribution and Natural History

Sibynomorphus oligozonatus is known from extreme southwestern Ecuador (Azuay and Loja Provinces) on the western slopes of the Andes and from a specimen without specific locality from Piura Department, Peru (Fig. 7). The known elevational range is 1,440 to 2,250 m.

The holotype of *Sibynomorphus oligozonatus* was found at night on the ground in the process of swallowing a small snail (Orcés and Almendáriz, 1989: 63) and in similar ecological conditions as specimens of *S. petersi*: "arid temperate zone with bushy vegetation that includes *algarrobos* and cacti; similar to the Brazilian caatinga and corresponding to the regions that Chapman called the arid temperate zone" (Orcés and Almendáriz, 1989: 63). *Algarrobos* refers to trees of the legume family, probably of the genus *Prosopis*, that are generally characteristic of seasonally dry to arid regions (e.g., mesquite). Chapman (1926: 97–98) described his "Arid Division of the Temperate Zone" thus:

> The aridity of the treeless portions of the Temperate Zone varies from that of valleys with sufficient rainfall to produce pasturage to that of rock-strewn plains where cactus is the prevailing type of vegetation. Generally speaking, the arid Temperate Zone comprises all the unforested areas between 9.000 and 12,000 feet, but where, because of insufficient rainfall, forests of the Subtropical Zone are lacking, the arid Temperate descends considerably lower and may even meet the Tropical Zone.

AMNH 110587 was dead on a road in an area of open grassy slopes in the Río Jubones valley (Charles W. Myers, personal communication, and field notes for 12 February 1974). Myers' notes describe this portion of the valley: "[from about 600 m to above 1,500 m] the Jubones valley has barren, steep, rocky slopes that are mostly covered with short grass and dotted with tree cacti. In places, especially along the river, there is low brush; some patches of sugar cane are grown in small flats near the river. . . . This section of the valley seems to be in rain shadow."

At the type locality (Orcés and Almendáriz, 1989) and in the Río Catamayo valley of southwestern Ecuador (BMNH 1935.11.3.108), *Sibynomorphus oligozonatus* is broadly sympatric with *S. petersi*. These species of *Sibynomorphus* are also broadly sympatric with another dipsadine, *Dipsas oreas*, but *D. oreas* may be segregated by habitat from the species of *Sibynomorphus* (see footnote 7).

Sibynomorphus oneilli Rossman and Thomas
Figures 8–12

Sibynomorphus oneilli Rossman and Thomas, 1979. Type locality: "NNE Balsas on the road to Abra Chanchillo, Departamento de Amazonas, Peru (ca. 1645 m)." Holotype, LSUMZ 33736. Rossman and Kizirian, 1993. Scrocchi et al., 1993. Carrillo de Espinoza and Icochea, 1995: 17.

Sibynomorphus oneilli has been reported in the literature from only two males (including the juvenile male holotype) and a female (Rossman and Kizirian, 1993; Rossman and Thomas, 1979). I examined these specimens and refer 14 additional specimens in the MUSM to *S. oneilli* (see *Specimens Examined and Locality Records*; another specimen provisionally referred to *S. oneilli* is excluded from this account because of its uncertain provenience: see detailed discussion of MUSM 2258 at the end of the species account for *S. vagrans*). The additional specimens significantly amplify knowledge of intraspecific variation and the distribution of *S. oneilli*. Of the three previously known specimens, Rossman and Thomas (1979: figs. 1, 2) illustrated the holotype and Rossman and Kizirian (1993: fig. 1) illustrated KU 212600. The third specimen,

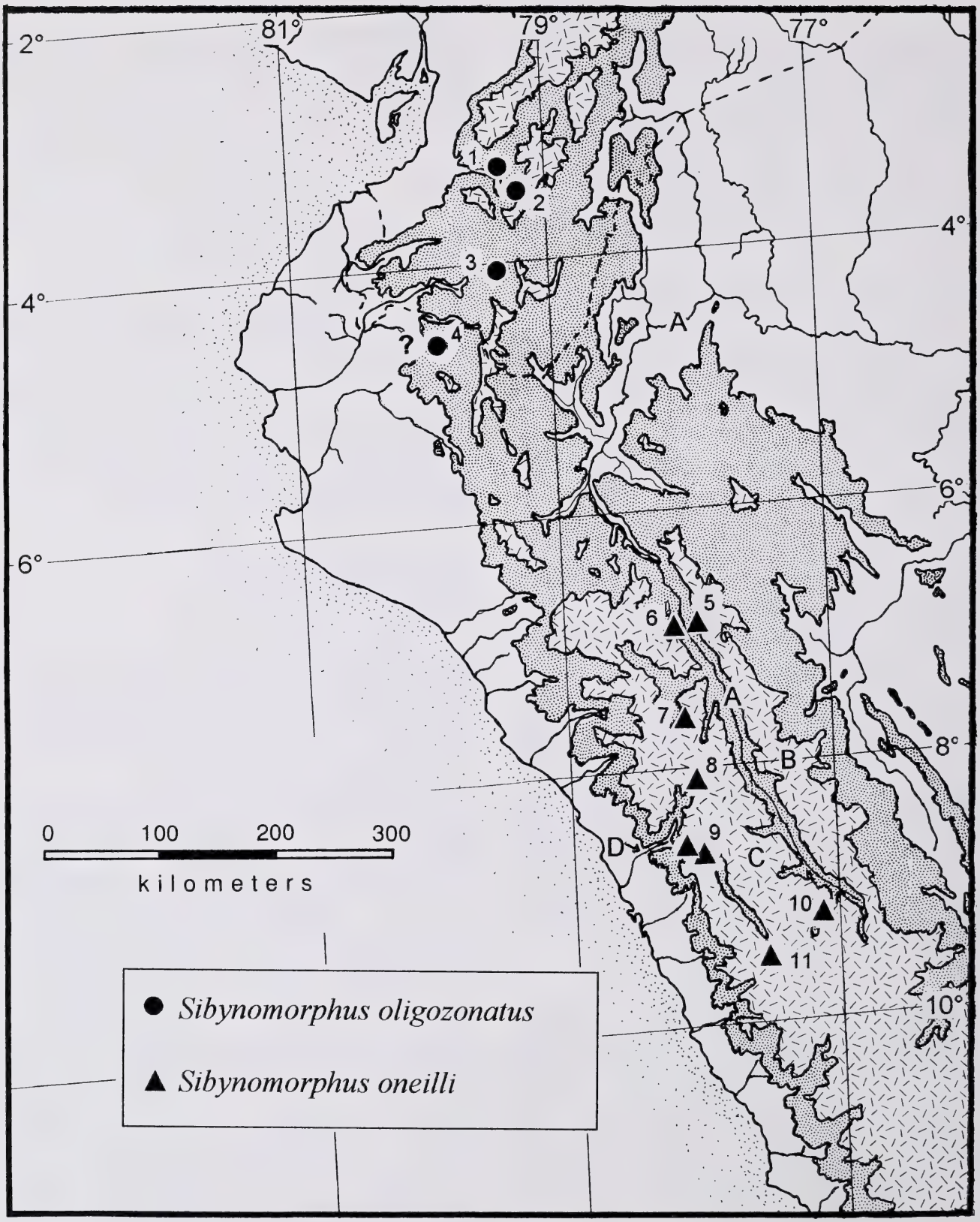


Figure 7. Distributions of *Sibynomorphus oligozonatus* and *S. oneilli* in southern Ecuador and northwestern Peru. All known localities are plotted (a couple of symbols reflect closely contiguous localities). See Figure 43 for amplification of the southern portion of the distribution of *S. oneilli* (Ancash Department, Peru). Stippled area is above 1,000 m; hatched area is above 3,000 m. Numbers are locality records and letters are physical features mentioned in the text, as follows: ***Sibynomorphus oligozonatus*:** *Ecuador:* (1) Santa Isabel; (2) Zhila (type locality); (3) Río Catamayo valley; *Peru:* (4) uncertain locality in Piura Department, Peru (symbol arbitrarily placed above the 1,000-m contour in the center of the department). ***Sibynomorphus oneilli*:** *Peru:* (5) between Balsas and Abra Chanchillo (type locality); (6) Abra Gelic; (7) Cajabamba; (8) Hacienda Ticapampa; (9) Huaylas and Hacienda Santa Rosa; (10) Yuracyacu; (11) Huaráz. **Physical features:** (A) Río Marañón (the inter-Andean portion is between the Cordilleras Oriental and Occidental; B and C, respectively); (B) Cordillera Oriental; (C) Cordillera Occidental; (D) Río Santa.

KU 212599, and others from the MUSM are illustrated herein (Figs. 8–12)

Notes on the Holotype and Comparisons with Other Specimens

Redescription of the Holotype. The following observations on the holotype (LSUMZ 33736) of *Sibynomorphus oneilli* were made in April 2004 and supplement the original description (Rossman and Thomas, 1979). Notes on the circumstances of its collection are given in the section *Natural History.* The type is compared with other specimens referred to this species, and a discussion of these specimens then follows.

The holotype is 233 mm in total length, 174 mm SVL (tail 25% of total length). It is a juvenile male, as indicated in the original description, but it has a distinct umbilical scar, which suggests that it is a very young juvenile. It is presently in rather poor condition. The specimen seems to have partially cleared since the species was described, perhaps as a result of the quality of its initial preservation and, possibly, exposure to a low concentration of isopropyl alcohol at some point during its history.[8] The clearing has resulted in loss of details of many aspects of the pattern and made some scale counts (e.g., ventrals) difficult to obtain with accuracy. For example, the head markings noted by Rossman and Thomas (1979: 5) are no longer discernible without magnification and careful observation, and the dorsal and ventral markings are very indistinct.

My scale counts for the holotype are very close or identical to those reported by Rossman and Thomas (1979): Dorsal scales 15–15–13, ventrals 168 (0 preventrals), subcaudals 77, anal plate single, preoculars 2/2, postoculars 2/2, primary temporals 1/1, secondary temporals 2/2, tertiary temporals 2/2, supralabials 8/8 (4–5 touching eye on each side), infralabials 9/8, maxillary teeth 16. The posterior dorsal scale reduction to 13 is unusual and seems to result from the "irregular fusions of the vertebral and paravertebral rows posteriorly" (Rossman and Thomas, 1979: 4); "irregular" in this case refers to the vertebral and paravertebral rows that are fused, then separated, several times with no particular regularity. On the posterior body, these fusions result in a "vertebral" row twice as wide as the adjacent rows, whereas anteriorly and at midbody, the vertebral row is scarcely wider than the adjacent paravertebral rows. Occasional reductions to 13 dorsal rows posteriorly occur in several other species of *Sibynomorphus* (e.g., *S. mikanii, S. neuwiedii,* and *S. turgidus*; Peters, 1960).

The top of the head has cleared substantially and, except under magnification, is medium to somewhat darker brown, forming a uniform head cap. Under magnification and with good light, the indistinct blotches on each parietal and the blotch on the frontal scale mentioned in the original description (Rossman and Thomas, 1979: 5) can be seen. The parietal blotches appear as broad elongate streaks parallel to the interparietal suture and extending from the anterior border of each parietal for most of the length of the scale. The uniform brown head cap is followed by a narrow pale collar and the first crossband. The body is grayish brown with narrow darker brown crossbands. The anterior neck band is about 2 scales wide. Subsequent crossbands are 1.5 scales wide, narrowing to less than 1 scale wide for most of the body. The posterior crossbands are very indistinct. Interspaces anteriorly are about 2 scales wide, broadening to 3 scales for most of body. The venter is largely cleared, but apparently had bold

[8] Details concerning the collection and initial preservation of the holotype are given in the section on natural history. Isopropyl alcohol, the standard storage medium of the LSUMZ collection, causes clearing of museum specimens at concentrations below 45% (Simmons, 2002: 70). The condition of the holotype of *Sibynomorphus oneilli* was not indicated in the original description, but the photographs provided and the description of the color pattern (Rossman and Thomas, 1979: 5) suggest that the clearing occurred subsequent to the original description.

squarish or half-moon–shaped spots aligned to form irregular lines on the lateral edges of the ventral plates.

Comparison of the Holotype with Other Specimens. The holotype of *Sibynomorphus oneilli* has several unusual characteristics compared with all other specimens referred to this species. These include ventral and subcaudal counts (168 and 77, respectively) at the upper extremities of the character ranges, an unusual reduction to 13 dorsal scales posteriorly (unique), 2/2 preoculars (unique), 9/8 infralabials (nearly unique: no other specimen had 8 infralabials, one other specimen had 9/9), and 1/1 primary temporals (nearly unique: one other individual had 1/1; another had one primary temporal on one side).

Some of these characters are unusual not only within *Sibynomorphus oneilli,* but within the genus as a whole. As a consequence of having two preoculars, the loreal is excluded from the border of the eye. The preocular scales appear to be normally formed and not merely the result of formation of an "extra" suture across a portion of the loreal, as occurs occasionally in Dipsadini (e.g., Cadle, 2005, fig. 1). Elsewhere within the genus, two preoculars occur with some frequency in *S. petersi* and *S. vagrans* (Table 1), and in another specimen of *S. oneilli,* the loreal on each side was divided to form two lower preoculars in addition to the usual one. The head scales of the holotype are roughly the same shape and proportions as in other specimens, although the parietals of the holotype extend farther laterally (correlated with it having only a single anterior temporal vs. two in most other specimens). However, it does not appear that an upper (second) anterior temporal is simply fused with the parietals in the holotype. Consequently, the head of the holotype appears somewhat long and narrow compared with other specimens.

The holotype differs in a few details of color pattern from other specimens although color patterns vary considerably within this species. The first dorsal crossband in the holotype is two dorsal rows wide. Subsequent crossbands are 1.5 rows wide, rapidly narrowing to one scale row wide for most of the body. In most other specimens, the anterior crossbands are three to five scale rows wide, narrowing to two scales (next four to five crossbands) and then to one scale row. In the holotype, bold blotches on the venter are confined primarily to the edges of the ventral plates, whereas in virtually all other specimens, the bold markings are distributed across the ventral plates (Figs. 9, 10, 12; Rossman and Kizirian, 1993: fig. 1). The holotype has a longitudinal dark streak on each parietal that parallels the interparietal suture, whereas in other specimens, the head is relatively unmarked or has streaks that parallel the posterolateral edge of the parietals.

New Material of *Sibynomorphus oneilli* from Ancash and Libertad Departments, Peru

After careful consideration of the characters and geographical setting of a series of *Sibynomorphus* in the MUSM from the Río Marañón and Río Santa drainages of the Andes in Ancash and Libertad Departments, Peru, I conclude that they conform to the concept of *S. oneilli* developed herein (Fig. 8).

As detailed in the section on distribution, *Sibynomorphus oneilli* inhabits a region of complex topography, and several major rivers and mountain chains separate the referred populations. Primary among these are the Río Marañón, which separates the type locality from all other known localities, and the Cordillera Blanca, which separates populations of the Amazonian and Pacific versants. Populations of the Pacific versant are known from the Río Santa drainage, a major river of the western Andes. This geographical setting and the relatively few specimens makes the interpretation of character variation within this species difficult. One locality (Yuracyacu) is represented by six specimens (four males, two females), but all other localities are represented by three or fewer specimens. The holotype of *S. oneilli* is the only

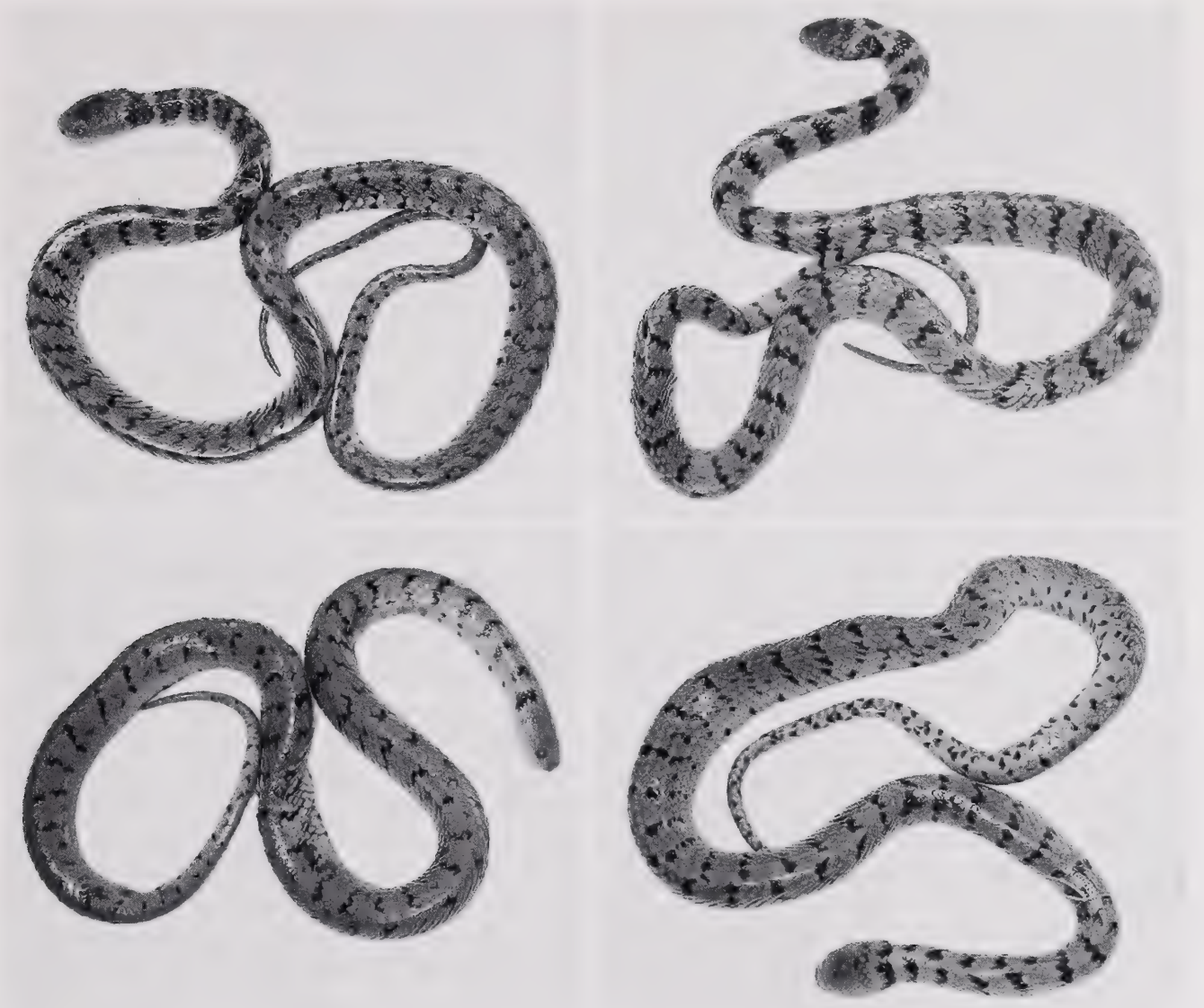


Figure 8. *Sibynomorphus oneilli.* Representative specimens in dorsal view. Top: left, MUSM 2770 (male, 470 mm SVL) from Hacienda Ticapampa (La Libertad Department); right, MUSM 3103 (female, 469 mm SVL) from Cajabamba (Cajamarca Department). Bottom: two specimens from Yuracyacu (Ancash Department): left, MUSM 3211 (female, 413 mm SVL); right, MUSM 3334 (male, 384 mm SVL).

specimen from east of the Río Marañón, and the type locality is the lowest elevation of all known localities (1,646 m). These factors might, in part, explain some of the unusual characters of the holotype. The complexity of the terrain inhabited by these populations enhances the potential for isolation and character differentiation among populations.

The "new" specimens from Ancash Department, herein referred to *Sibynomorphus oneilli,* were perplexing because they extend the range of variation in scutellation and other characters within *S. oneilli.* In some cases, the extended ranges approach the character variation within *S. vagus.* Many of these specimens are much larger (nine of 14 specimens >500 mm total length, with the largest 790 mm total length) than had been known for *S. oneilli* from the three previously known specimens (233–374 mm total length). Further complicating their interpretation was the existence, in the Río Santa valley, of specimens lacking discrete crossbands, a characteristic of many of the known specimens of *S. vagus* (see species account). Thus, whether the "new" specimens represented

S. oneilli, S. vagus, some mixture of the two, or even a new species, was a real question.

All specimens from east of the Cordillera Blanca (10 specimens, including the holotype from east of the Río Marañón) show the banded pattern considered typical of *Sibynomorphus oneilli* (Rossman and Kizirian, 1993; Rossman and Thomas, 1979) (Fig. 8). Of seven specimens from the Río Santa drainage (localities Huaylas, Hacienda Santa Rosa, Hacienda Ticapampa, and Huaráz), three are typically banded (MUSM 2770, 3089, 3395) and one has very narrow and fragmented dorsal crossbands (MUSM 2662). The other three specimens, each from a different Río Santa locality, lack crossbands entirely: MUSM 2687 (Huaylas), 2390 (Hacienda Santa Rosa), and 2660 (Huaráz). Instead, they have a dorsal pattern of fine dark flecks and reticulations reminiscent of the dorsal pattern in *S. vagus* and some specimens of *S. petersi.* Two lines of reasoning led to the conclusion that all specimens from the Río Santa valley and from Yuracyacu in southern Ancash were referable to *S. oneilli.*

First, although the Cordillera Blanca is an impressive mountain range, it is also geologically quite young and probably attained heights over 3,000 m only since the late Miocene (Farrar and Noble, 1976; Simpson, 1979). Geographically, it would not be surprising that populations on either side of the Cordillera Blanca would be closely related to one another. On the other hand, it seems less likely that populations in the Río Santa valley would be closely related to populations on the Amazonian versant far to the north overshadowed by the Cordillera de Huancabamba (the range of *Sibynomorphus vagus*). Populations of the Río Santa are separated from those of Huancabamba not only by rugged mountains, but also by the relatively lower elevations of the Huancabamba Deflection region. This area is a biogeographic discontinuity to many montane elements of flora and fauna that reach their northern or southern distributional limits here (Duellman, 1979; Lynch, 1986; Simpson, 1975, 1979).

Second, the character variation within the sample from the Río Santa valley is more similar to *Sibynomorphus oneilli* than to *S. vagus* (Table 3), despite the similarity of some individuals to *S. vagus* in color pattern. Banded specimens throughout Ancash and southern Cajamarca/Amazonas Departments (e.g., Figs. 8, 9) resemble the regular and fully crossbanded pattern typical of *S. oneilli* in scutellation as well as pattern, rather than the unbanded or anteriorly banded patterns typical of *S. vagus.* A comparison of selected characters of the unbanded specimens of *Sibynomorphus* from the Río Santa valley with both *S. oneilli* and *S. vagus* (Table 3) shows that for ventral counts, unbanded males and females from the Río Santa are within the range of other specimens of *S. oneilli,* but outside the range for *S. vagus.* There are strong frequency differences between *S. oneilli* and *S. vagus* with respect to temporal scale counts. Temporal scale patterns in the unbanded specimens from the Río Santa correspond to the predominant frequencies in *S. oneilli* rather than *S. vagus.* Furthermore, some specimens referred to *S. oneilli* from east of the Cordillera Blanca have fragmented dorsal bands (Fig. 8, lower left), which suggests that there is some lability in the expression of crossbands. I conclude that all available specimens from both sides of the Cordillera Blanca in Ancash Department are referable to *S. oneilli* and that this species is polymorphic in color pattern, as is already well known for some other species of *Sibynomorphus.*

Diagnosis

Sibynomorphus oneilli has a large number (38–63) of dark crossbands on the dorsum throughout the length of the body when discrete crossbands are present (the most common condition) (Fig. 9). In some specimens, the dorsal crossbands are complete only anteriorly; the posterior cross-

Table 3. Comparison of selected characters of noncrossbanded specimens referred to *Sibynomorphus oneilli* from the Río Santa valley with character states in *S. oneilli* and *S. vagus*. Ventral counts summarized for *S. oneilli* and *S. vagus* are ranges followed by mean (in parentheses) and sample sizes (*N*). Temporal counts for these two species treat each side of each specimen as an independent observation. Bilateral counts are separated by a solidus (left/right). The sample of *S. oneilli* includes all specimens except those from the Río Santa valley. See Table 1 for summary statistics of these data.

	Noncrossbanded Specimens from the Río Santa Valley				
	MUSM 2687 Female Huaylas	MUSM 2390 Female Santa Rosa	MUSM 2660 Male Huaráz	*Sibynomorphus oneilli* (except Río Santa)	*Sibynomorphus vagus* (total sample)
Ventrals					
Male	—	—	159	156–168 (163) $N = 8$	144–152 (149) $N = 5$
Female	163	168	—	163–173 (168) $N = 4$	151–158 (154) $N = 5$
Primary temporals	2/2	2/2	2/1	2 ($N = 18$)	1 ($N = 19$) 2 ($N = 1$)
Secondary temporals	3/3	3/3	3/3	2 ($N = 2$) 3 ($N = 14$) 4 ($N = 4$)	2 ($N = 18$) 3 ($N = 2$)
Tertiary temporals	4/3	3/3	4/4	2 ($N = 2$) 3 ($N = 6$) 4 ($N = 11$)	0 ($N = 0$) 1 ($N = 1$) 2 ($N = 13$) 3 ($N = 5$)

bands in these specimens are incomplete middorsally and appear as narrow lateral bars. Several specimens from the Río Santa valley lack discrete bands entirely; instead, the dorsum has an obscure network of dark flecks or reticulations. The anterior crossbands (generally two to three dorsal rows wide) are slightly broader than, or equal in width to, the interspaces, whereas most crossbands are only one dorsal row wide and much narrower than the interspaces. The venter is heavily checkered or spotted with large bold markings (rounded, squarish, or half-moon–shaped) (Fig. 9). Ventrals are 152–168 in males; 163–173 in females. Subcaudals are 62–77 in males; 56–64 in females. Infralabials are 9–13.

Sibynomorphus oneilli differs from other species of *Sibynomorphus* in Ecuador and Peru as follows. In *S. oligozonatus*, *S. vagrans*, and *S. williamsi*, the anterior crossbands are usually twice or more as broad as the interspaces (see illustrations in the species accounts), whereas in *S. oneilli*, crossbands are usually equivalent to, or narrower than, the interspaces (occasionally broader than interspaces but never approaching twice their width). These species also differ from *S. oneilli* in other characters: *S. oligozonatus* has fewer supralabials (6–7) and a less boldly patterned venter (Figs. 1, 2, 4, 6). *Sibynomorphus williamsi* has fewer supralabials (6–7) and a greater number of ventrals (males, 173–182; females, 181–188) than *S. oneilli*. *Sibynomorphus oneilli* averages about 10 more ventrals and 15 fewer subcaudals than *S. vagrans* when sexes are considered separately (Table 1).

Sibynomorphus vagus differs from *S. oneilli* in temporal scale patterns (Table 1) and by having fewer ventrals (males, 144–152; females, 151–158). *Sibynomorphus petersi* has a greater number of ventrals (164–188, sexes combined) and subcaudals (males, 75–87; females, 65–77) than *S. oneilli* and has different color patterns on the head and body.

Description

Size and Scutellation. Taxonomic data for *Sibynomorphus oneilli* are summarized in Table 1. The largest specimen is a female 790 mm total length (624 mm SVL).

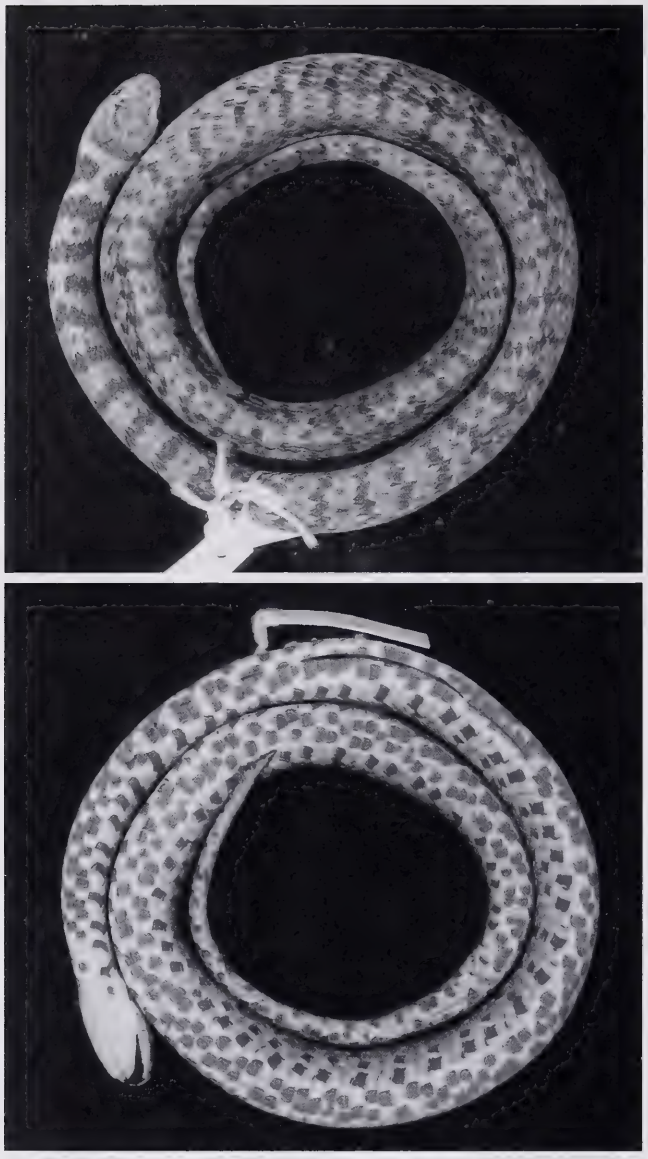


Figure 9. *Sibynomorphus oneilli.* Dorsal and ventral views of KU 212599 (from near Cajabamba, Cajamarca Department, Peru). Female, 374 mm total length.

The largest male is 571 mm total length (440 mm SVL). Body somewhat compressed. Tail 22–26% of total length in males, 20–22% of total length in females. Dorsal scales smooth and in 15–15–15 rows in all specimens except the holotype, in which there is a posterior reduction to 13 scale rows (see above *Redescription of the Holotype*). Vertebral row slightly broader than paravertebral rows. Ventrals 152–168 (averaging 161) in males, 163–173 (averaging 167) in females; 0–4 preventrals precede the ventral plates. Anal single. Subcaudals 62–77 (averaging 68) in males, 57–64 (averaging 61) in females.

Usually, a loreal and a single preocular (superior to the loreal) border the anterior edge of the eye, but the preocular is often fused with the prefrontal (Table 1); loreal squarish or polygonal. The holotype has two preoculars on each side and the loreal is separated from the eye (interposed between the inferior preocular and the posterior nasal). MUSM 3376 has a separate preocular but, in addition, the loreal is divided vertically and horizontally to form a pair of lower preoculars, thus resulting in three preoculars. Postoculars are virtually always 2 (3 on one side of one specimen). Primary temporals usually 2 (occasionally 1); secondary temporals usually 3 (range 1–4), tertiary temporals usually 3 or 4 (rarely 2). Supralabials 6–10 with the most frequent patterns 8 (4–5 bordering eye) or 7 (3–4 bordering eye). Infralabials 9–13 (most frequently 10 or 11). One pair of infralabials in contact behind mental in all specimens. Chin shields in 2 pairs (N = 3), 3 pairs (N = 10), 3.5 pairs (N = 1), or 4 pairs (N = 4). Maxillary teeth 13–16 (N = 13). The pupil is prolate in preservative.

Barring patterns of geographic variation that remain unforeseen because of sampling issues,[9] *Sibynomorphus oneilli* shows typical colubrid patterns of sexual dimorphism in size (females attain larger size), ventral counts (female greater; t = 2.545, df = 15, $p < 0.05$), subcaudal counts (male greater; t = 2.764, df = 12, $p < 0.05$), and relative tail length (males have longer tails) (Table 1).

Color in Life. Unknown.

Color in Preservative. The pattern of the holotype is described above, but its poor state of preservation does not warrant a detailed description (see above *Rede-*

[9] The female from Santa Rosa is substantially larger than other specimens (790 mm total length). Large size is conceivably characteristic of this population, but that is unverifiable with a single specimen. It could be that the extremely large size of this specimen is due to vagaries of sampling. The next largest specimen, a male, was 623 mm total length.

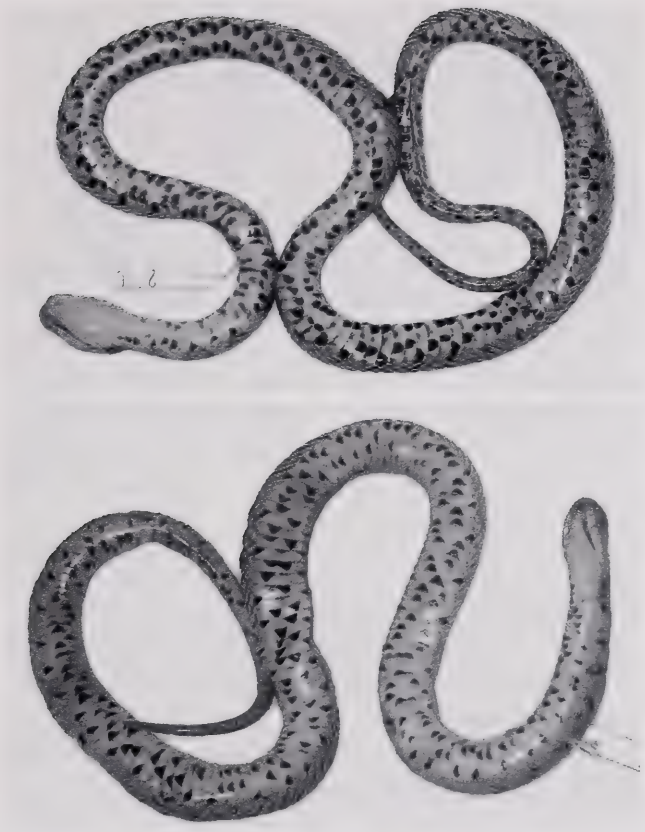


Figure 10. *Sibynomorphus oneilli.* Representative specimens in ventral view. Top: MUSM 2770 (La Libertad Department; male, 470 mm SVL). Bottom: MUSM 3211 (Ancash Department; female, 413 mm SVL).

Figure 11. *Sibynomorphus oneilli.* Dorsal and lateral views of head, KU 212599. The skull of this specimen had been dissected from the skin, hence the appearance of the eyes and tears in the rostral and mental regions.

scription of the Holotype and Rossman and Thomas, 1979: 5). The coloration of *Sibynomorphus oneilli* in preservative, on the basis of the other specimens, follows. Dorsal ground color medium brown or grayish brown, occasionally somewhat reddish brown; grayish when the stratum corneum is removed. Dorsal crossbands and other markings black (Figs. 8, 9). Dorsal crossbands on the body, when present, range from 38 to 63 with no apparent sexual dimorphism; crossbands can be fragmented or even completely absent, as described below. The venter is dull whitish or with fine dark stippling giving a dusky appearance, upon which are bold black squarish or half-moon–shaped spots in a checkerboard pattern. Ventral spots are usually densely arrayed (Figs. 9, 10), but there is a tendency for specimens lacking dorsal bands also to have less boldly patterned venters (see Fig. 12). Gular region immaculate, grayish to white. Dorsal and ventral surfaces of the tail are like the corresponding surfaces of the body, except the dorsal bands are incomplete middorsally.

The top of the head is medium brown, usually with some scattered irregular blackish marks primarily on the parietals and frontal; these marks sometimes include an irregular curved black streak that roughly parallels the posterolateral edge of each parietal (Fig. 11; Rossman and Kizirian, 1993: fig. 1). A narrow dark nape bar is frequently present between the first dorsal crossband and the parietal scales; it extends laterally to just above the posterior supralabials and, when present, can be manifested by dusky shading or a very distinct blackish bar. In a few specimens, the top of the head is unmarked (e.g., MUSM 3211, Fig. 8). Temporal scales are very narrowly edged with black, but without close examination, the impression is that the side of the head is unmarked. The supralabials are dull whitish with some dark stippling (but no discrete markings) along

Figure 12. *Sibynomorphus oneilli.* A nonbanded specimen from Huaylas in the Río Santa valley (Pacific versant, Ancash Department). MUSM 2687 (female, 463 mm SVL).

suture lines. Infralabials are dull whitish, unmarked.

The dorsal pattern varies by individual. The first crossband is interrupted middorsally in many specimens, forming a pair of blotches (much higher than wide) on the side of the neck (Figs. 8 [upper and lower right], 9, 11). Other crossbands on the body are likewise sometimes interrupted middorsally. At least occasionally (e.g., MUSM 3211; Fig. 8, lower left), virtually all of the crossbands are interrupted so that the dorsal pattern consists of a series of irregular narrow vertical streaks on the flanks, and in extreme cases (MUSM 2662), the crossbands are extremely fragmented so as to give the appearance of an irregular pattern. In most specimens, the crossbands on the anterior quarter to third of the body are wider than more posterior crossbands (Figs. 8, 9). Occasionally (MUSM 2770, KU 212600) these anterior crossbands are twice or more the width of the posterior crossbands. Except for these anterior bands, most bands on the body are one scale row or less in width and are much narrower than the interspaces. As described above (*New Material of* Sibynomorphus oneilli *from Ancash and Libertad Departments, Peru*), two females and a male from the Río Santa valley lack crossbands entirely and have irregular dark flecks over the dorsum (Fig. 12).

There seems to be little or no ontogenetic change in color pattern, as four specimens 203–280 mm total length had patterns similar to adults; one of these (MUSM 3089; 232 mm total length) had the highest number of dorsal bands recorded (63), and these were formed by darkened scale edges rather than fully formed bands.

Details of the dorsal patterns of KU 212599 and 212600 are as follows:

KU 212599 (Fig. 9): Approximately 55 crossbands are present on the body. On the neck just behind the head is a pair of lateral blackish blotches 4 to 5 dorsal rows wide. The following crossband (complete across the dorsum) is 3 scales wide and the following 4 crossbands are two scales wide. Subsequent crossbands are no more than a single dorsal row wide, becoming increasingly fragmented posteriorly, but more or less discrete the length of the body. Anteriorly, the crossbands extend down to the first dorsal row or outer edge of the ventrals; posteriorly the crossbands tend to fragment before reaching the first dorsal row. Interspaces between the crossbands are medium reddish brown, 2 to 3 dorsal rows in width anteriorly and usually 3 rows posteriorly. Many dark flecks are present in the interspaces, especially posteriorly.

KU 212600: The body has 38 total crossbands (+2 half-bands in between complete bands) (see Rossman and Kizirian, 1993: fig. 1 for dorsal and ventral photographs of this specimen). Crossbands are complete across the dorsum (except the two half-bands) and extend to the outer edge of the ventral plates, where most fuse more or less completely with one or more of the dense squarish spots on the venter. The first crossband behind the head is 4 scales wide, the next five bands are 3 scales wide, the following five are two scales wide, and the rest are one scale wide. The crossbands are wider middorsally than ventrally; they have irregular edges, but are essentially oriented vertically (slightly curved in some cases). Laterally, between

many of the crossbands, and in the vertebral/paravertebral region are scattered irregular black flecks mainly formed by black edging on some of the dorsal scales. Interspaces anteriorly are two scale rows wide, broadening to three on anterior one-third of body, and then to four scale rows wide posteriorly.

Etymology. Sibynomorphus oneilli was named for ornithologist John P. O'Neill, who collected the holotype. The ornithological expeditions of Louisiana State University to Peru, many under the guidance of O'Neill, have also made important contributions to knowledge of the Peruvian herpetofauna.

Distribution

Sibynomorphus oneilli is known from the northern end of the Cordillera Oriental in extreme southern Amazonas Department, Peru, and in the Cordillera Occidental from southern Ancash to southern Cajamarca Department (Fig. 7; see also Fig. 43). Localities are on the Amazonian versant (Río Marañón drainage) and Pacific versant (Río Santa and its tributary, the Río Tablachaca/Tablache) of the Andes. The recorded elevational range is 1,646–3,500 m. In Ancash Department, populations of *S. oneilli* from the Amazonian versant of the Cordillera Occidental are separated from populations of the Pacific versant (Río Santa drainage) by extensive mountains of the Cordillera Blanca well over 4,000 m. The type locality is separated from other known localities by the Río Marañón (but see footnote 15).

As here conceived, populations of *Sibynomorphus oneilli* inhabit one of the most tectonically active and topographically complex regions of the Andes. The species occurs on both sides of the Río Marañón, one of the longest and largest rivers descending from the Andes; it separates the Cordillera Oriental from the Cordillera Occidental, the principal chains of the Andes in northern Peru. The Río Marañón flows northwesterly until near the Ecuadorian border, thence turning east and becoming the major western affluent of the Amazon system. On the Pacific versant, *S. oneilli* occurs in the valley of the Río Santa and one of its tributaries, the Río Tablachaca/Tablache (which forms the border between Ancash and La Libertad Departments). The Río Santa flows northwesterly through the length of Ancash Department, eventually turning westward through the gorge of the Cañon del Pato and emptying into the Pacific Ocean. Lehr et al. (2002: fig. 11) present a photograph of the Río Santa valley upstream from Huaráz, one of the localities for *S. oneilli*. The inter-Andean valleys of the Río Marañón and Río Santa are relatively arid and presently form effective barriers for east–west dispersal of montane flora and fauna (Simpson, 1979).

In addition to large river systems, populations of *Sibynomorphus oneilli* are separated by incredibly rugged mountains. Populations in the Río Marañón drainage are separated from those in the Río Santa valley by the glacier-laden Cordillera Blanca, the highest continuous range in the Andes (see Lehr et al., 2002: fig. 11). This impressive mountain chain contains more than 10 peaks exceeding 6,000 m elevation (the highest being Nevado Huascarán at 6,746 m) and no passes below 4,000 m; most of its area is above 5,000 m (Clapperton, 1993). Vertical descents on either side of the Cordillera Blanca frequently exceed 4,500 m, and its fault zones are young and very active (Noble et al., 1990). Major uplifts in the late Miocene through Pleistocene brought the mountains to their present height (Farrar and Noble, 1976). The Río Marañón and the Río Santa are relatively young rivers that developed in the down-faulted trenches between major uplifts of the Cordillera Oriental and Cordillera Occidental (Río Marañón) or within the Cordillera Occidental (the Río Santa, flanked on the east and west by the Cordillera Blanca and Cordillera Negra, respectively).

Thus, populations referred to *Sibynomorphus oneilli* on either side of major geographic barriers within the species' range (Río Marañón, Cordillera Blanca)

were probably isolated, geologically speaking, relatively recently. Nonetheless, the heavily dissected topography enhances opportunities for the isolation of these populations, particularly those of the eastern and western versants, which are separated by inhospitable terrain or unsuitable high-elevation habitats. *Sibynomorphus oneilli* is one of few reptiles known to have populations on both the Amazonian and Pacific versants of the Andes, and most of these have only become known in conjunction with field work in the area in the last quarter century (Cadle, unpublished data).

Natural History

The holotype of *Sibynomorphus oneilli* was collected 8 August 1975 in "semiarid brushland" (Rossman and Thomas, 1979). According to the collector, ornithologist John P. O'Neill (personal communication, 25 April 2006), the holotype was dead in the middle of a gravel highway on an overcast, cool day; the area had scattered bushes and was rather overgrazed. It was placed in a jacket pocket for 24 or more hours before preservation, which could in part explain its poor present condition.

Two specimens (KU 212599–600) were collected in January and March under rocks in agricultural land (Rossman and Kizirian, 1993). Other specimens with dates of collection have been obtained in January, February, March, April, September, October, and December. These months generally correspond to the cooler, wetter part of the year in this portion of the Andes (wet season primarily November–April).

The three smallest individuals have visible umbilical scars: MUSM 3303 (203 mm total length; 155 mm SVL), MUSM 3089 (232 mm total length; 181 mm SVL), and LSUMZ 33736 (233 mm total length; 174 mm SVL). MUSM 3089 was collected in December 1982; LSUMZ 33736 was collected 8 August 1975. The date of collection of MUSM 3303 is unknown.

Sibynomorphus petersi Orcés and Almendáriz Figures 13–27

Dipsas mikanii oreas: Parker, 1934: 271, 1938: 444 (misidentifications). See later discussion of misidentified literature records.

Dipsas variegata variegata: Peters, 1964: 47 (misidentification). Based on USNM 237040, which was subsequently referred to *Sibynomorphus petersi* (Cadle and Myers, 2003: 7).

Sibynomorphus petersi Orcés and Almendáriz (1989). Type locality: "Zhila (2,250 m) 79°17′26″W, 03°39′45″S [see footnote 19], parroquia Oña, cantón Girón, Provincia Azuay [Ecuador]." Holotype, EPN 2659. Almendáriz and Orcés (2004).

Sibynomorphus vagus: Lehr et al. (2002) (misidentification of SMF 80048, MUSM 20583).

Notes on the Type Series of *Sibynomorphus petersi*

The specimens here referred to *Sibynomorphus petersi* substantially amplify knowledge of variation in this taxon, which was previously reported only from the holotype (EPN 2659) and two paratypes (EPN 1847, 2660) (Orcés and Almendáriz, 1989). I refer other specimens from southern Ecuador and eight Peruvian specimens to this species (see *Specimens Examined and Locality Records*). Of the type series, I have examined only a paratype from the type locality, EPN 2660 (Fig. 13).

According to Orcés and Almendáriz (1989) the holotype is an adult male 763 mm total length, 609 mm SVL, 154 mm tail length (= 20.2% of total length and not the 21.9% reported in the original description); 15 [midbody] dorsal scale rows (vertebral row slightly enlarged); 176 ventrals, 79 subcaudals, single anal; 9 supralabials (4 + 5 touching the eye), 12 infralabials; four pairs of chin shields; 0/1 preoculars, 2/2 postoculars; 3 + 2 + 3/2 + 3 + 3 temporals. These data conform to my own for male *Sibynomorphus petersi* (Table 1), except that the tail is shorter than in any male I examined.

Diagnosis

Sibynomorphus petersi attains a large size (to 771 mm total length in females, 763 mm in males) and has moderately

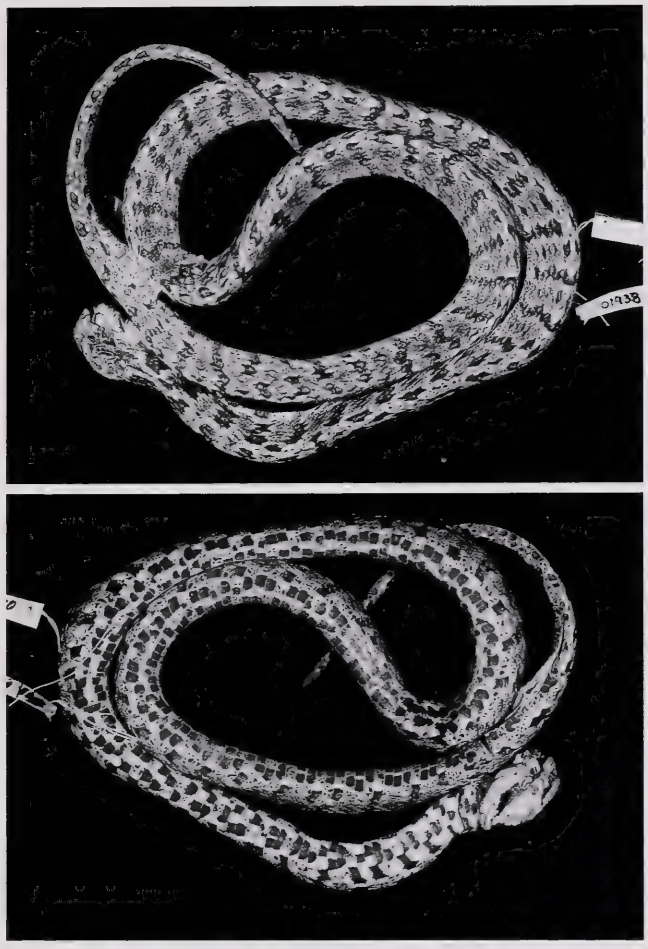


Figure 13. *Sibynomorphus petersi.* Paratype (EPN 2660, Azuay Province, Ecuador) in dorsal and ventral views. Female, 542 mm SVL.

high ventral (164–188) and subcaudal (65–87) counts. Many features distinguishing this species from others in Peru and Ecuador are aspects of color pattern. *Sibynomorphus petersi* has a dorsal ground color of medium brown (brown or grayish in preservative), generally with narrow, dark brown (sometimes dark gray in preservative), irregular zigzag crossbands that extend ventrally to the lowermost dorsal rows or extreme outer edges of the ventral scales (Figs. 13, 14). Three or four anterior crossbands are sometimes broader than the others. Crossbands may be fragmented into a dorsal and lateral series of blotches, and crossbands or blotches are difficult to discern in some individuals. The venter is whitish with bold black or dark brown squarish or half-moon–shaped blotches or streaks; the ventral ground color is sometimes heavily invested with brown, a reflection of a dense peppering of minute flecks and spots.

The top of the head is brown or grayish brown with dark brown spots, streaks, or other markings in a highly irregular pattern. Nonetheless, one feature of the head pattern seems relatively constant, albeit somewhat variable in precise execution: a large discrete spot is usually present on each prefrontal scale (Fig. 15). The prefrontal spots are usually symmetrically placed but vary in size, shape, and exact position among specimens (see *Color in Preservative and Variation in Pattern*). They are usually round but occasionally are irregular in shape. Dark markings on the head have a narrow pale edge (yellowish in life), which can be obscure in preserved specimens. In many specimens the dark head markings also have a pale core (Fig. 15).

Sibynomorphus petersi differs from other species of the genus in northern South America as follows: *S. vagrans* and *S. vagus* have fewer ventrals (149–159 and 144–158, respectively) and different color patterns (see descriptions and illustrations herein). *Sibynomorphus oneilli* usually has narrow, more or less straight-sided (compared with zigzag) crossbands and has fewer ventrals and subcaudals than *S. petersi* (*S. oneilli* ventrals and subcaudals, male: 152–168 and 62–77; female: 163–173 and 57–64). *Sibynomorphus oligozonatus* has anterior crossbands that are much broader than the interspaces and, in males, fewer ventrals (145–163) and subcaudals (66–68); *S. oligozonatus* has six or seven supralabials, whereas *S. petersi* usually has eight. *Sibynomorphus williamsi* usually has six supralabials (3–4 touching the eye), whereas *S. petersi* usually has eight supralabials (4–5 touching the eye); *S. williamsi* also has distinct bold crossbands the entire length of the body and usually a relatively unmarked venter (when marked, never bold spots or half-moons).

In the collections I surveyed, *Sibynomorphus petersi* was commonly misiden-

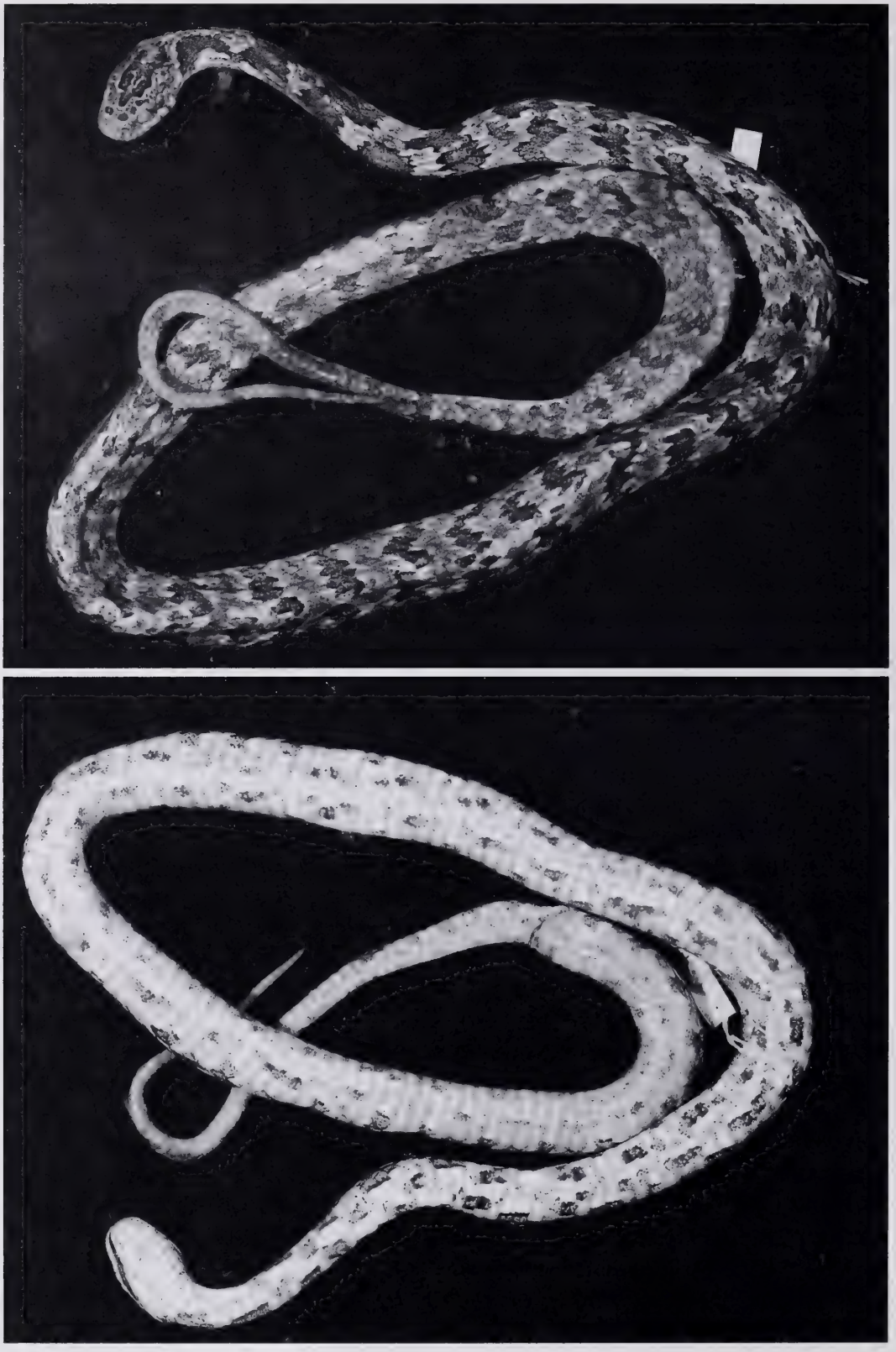


Figure 14. *Sibynomorphus petersi.* Dorsal and ventral views of a specimen from southern Ecuador. EPN 4737 (Loja Province, Ecuador). Female, 580 mm SVL.

Figure 15. *Sibynomorphus petersi.* Top: Lateral view of head (BMNH 1900.3.30.19 from San Pablo, Cajamarca Department, Peru). Bottom: Dorsal view of head (EPN 4737, Loja Province, Ecuador). Both specimens show the large spot on each prefrontal scale that is characteristic of *S. petersi* despite some variation (see Figs. 19, 22). In most specimens, the spots are bordered by a narrow pale ring, as seen clearly in the lower figure here. Note also the minute dark spots on individual scales.

tified as *Dipsas variegata* or *D. oreas* (see discussion of misidentifications in the literature below). *Sibynomorphus petersi* can be distinguished from all species of *Dipsas* in western Ecuador and Peru by a few key aspects of color pattern, especially details of the banding pattern on the body and patterns atop the head (see Cadle, 2005; Cadle and Myers, 2003). Scutellation characters alone are insufficient for some comparisons because of substantial overlap in scale counts for many species of Dipsadini. Species of *Dipsas* also have a relatively much larger eye than species of *Sibynomorphus*; see Cadle (2005) and Cadle and Myers (2003) for descriptions and illustrations. The following comparisons show, for subadult and adult *S. petersi* and *D. oreas*, the difference in eye size compared with SVL (for these comparisons subadults are ≤351 mm SVL):

S. petersi:
Adult eye size: 0.552 ± 0.081% SVL (N = 4)
Subadult eye size: 0.701 ± 0.016% SVL (N = 2)

D. oreas:
Adult eye size: 0.730 ± 0.049% SVL (N = 12)
Subadult eye size: 0.840% SVL (N = 1)

Misidentifications of Sibynomorphus petersi *in the Literature. Sibynomorphus petersi* was frequently misidentified in museum collections, and some of these records have made their way into the literature. Parker (1934: 271; 1938: 444) identified specimens of *S. petersi* from the collections of Clodoveo Carrión from southern Ecuador as *Dipsas mikanii oreas* (= *D. oreas*). Parker cited only six specimens from the Carrión collection as this species, whereas I located 13 Carrión specimens in the BMNH that were originally identified as "*Dipsas mikanii oreas.*" All of these except one are here referred to *S. petersi* (the other is *S. oligozonatus*; see *Specimens Examined and Locality Records*). Three specimens can, with reasonable confidence, be associated with BMNH catalogue numbers on the basis of the sex, locality, and segmental counts provided by Parker (1938): a male and two females from "Catamayo Valley" are, respectively, BMNH 1935.11.3.110 (= *Sibynomorphus petersi*), 1935.11.3.108 (= *S. oligozonatus*), and 1935.11.3.109 (= *S. petersi*). I could not confidently associate BMNH numbers with the other three specimens reported by Parker (1934, 1938).

Specimens of *Sibynomorphus petersi* were commonly misidentified as *Dipsas variegata,* apparently on the basis of earlier reports of that species from Ecuador and Peru (e.g., Peters, 1960, 1964). However, Cadle and Myers (2003) showed that some previously published records of

"*Dipsas variegata variegata*" and "*Dipsas variegata nicholsi*" from Ecuador and Peru were based on misidentifications of other species, including *D. andiana, D. oreas, D. peruana,* and *S. petersi.*[10] Peters' (1964: 47) record of "*Dipsas variegata variegata*" from western Ecuador is based on USNM 237040, which was subsequently referred to *Sibynomorphus petersi* (Cadle and Myers, 2003: 7). Lehr et al. (2002) referred two specimens of *S. petersi,* SMF 80048 and MUSM 20583 from Ancash Department, Peru, to *S. vagus.* They clearly are not that species and one of them is here referred to *S. petersi* (see footnote 22).

[10] Cadle and Myers (2003) were specifically concerned with Peruvian and Ecuadorian records of *Dipsas variegata* discussed by Peters (1960, 1964) and Steindachner (1902). We failed to note more recent reports of "*D. variegata*" from southeastern Peru (Doan and Arriaga, 2002; Duellman and Salas, 1991). In 2001, I had examined one of two specimens referred to *D. variegata* from Cusco Amazónico (Duellman and Salas, 1991), KU 214858, and concluded that it is not the same taxon as *D. variegata* Duméril, Bibron, and Duméril from Venezuela and the Guayanan region. On this basis, Duellman (2005: 371) listed the Cusco Amazónico material as "*Dipsas* sp." Doan and Arriaga (2002) apparently collected the same taxon from a site near Cusco Amazónico and referred all the material to *D. variegata.*

KU 214858 (Duellman, 2005: 371 and pl. 183), a female, has more ventrals and a different color pattern than specimens of *Dipsas variegata* from Venezuela and the Guayanan region examined by Cadle and Myers (2003: table 1), although ventral counts recorded in the literature, including those for a syntype reported in the original description, are greater (Cadle and Myers, 2003: footnote 5; Duméril et al., 1854: 478). KU 214858 is similar in color pattern and high ventral counts to specimens tentatively referred to *D. variegata* from the mouth of the Amazon (Cadle and Myers, 2003: footnote 5; Cunha and Nascimento, 1993). This taxon has not turned up in some comprehensive collections from central Amazonia (Martins and Oliveira, 1998). Clearly, the status of these specimens from southeastern Peru referred to *D. variegata* (Doan and Arriaga, 2002; Duellman and Salas, 1991) needs clarification, and *Dipsas variegata* itself needs a thorough range-wide study. These issues do not affect Cadle and Myers's (2003) conclusions on the basis of Peters' (1960, 1964) and Steindachner's (1902) records of "*Dipsas variegata*" from Peru and Ecuador, none of which are that species.

Description

Size and Scutellation. Table 1 summarizes basic characteristics of *Sibynomorphus petersi.* The largest specimen is a female 771 mm total length, 595 mm SVL. The largest male is the holotype, 763 mm total length, 609 mm SVL (Orcés and Almendáriz, 1989). Tail 22–28% of total length in males (with the holotype an outlier at 20% on the basis of measurements in the original description), 20–24% of total length in females. Body somewhat compressed. Dorsal scales smooth, in 15–15–15 rows. The vertebral row is slightly broader than, to approximately twice the width of, the adjacent paravertebral rows; the vertebral row seems relatively broader in Ecuadorian compared with Peruvian specimens. Ventrals 164–183 (averaging 173) in males, 173–188 (averaging 179) in females. Ventrals preceded by one to three preventrals. Anal single. Subcaudals 75–87 (averaging 81) in males, 65–77 (averaging 73) in females. Usually a loreal and a single preocular border the eye (preocular superior to the loreal); occasionally two or three preoculars were present, but the preocular was never fused with the prefrontal (Table 1). The loreal varies in shape from squarish (e.g., Fig. 15, top) to more elongate (Fig. 23, bottom). Postoculars 2 (rarely 3). Primary temporals usually 2 (occasionally 1). Secondary temporals usually 3 (range 2–4). Tertiary temporals 2–4. Supralabials usually 8 (range 7–9) with 4–5 bordering the eye. Infralabials usually 10 or 11 (range 9–12). One or two pairs of infralabials in contact behind the mental, with the following frequencies in the sample: first pair of infralabials in contact (11), first two pairs in contact (6), one infralabial contacts two on the opposite side (4). Three pairs (N = 15), 3.5 pairs (N = 1), or four pairs (N = 3) of squarish or polygonal chin shields. Maxillary teeth 14–17 (N = 10).

Sexual Dimorphism. Compared with females, male *Sibynomorphus petersi* have significantly fewer ventrals (t = 2.408, df

= 22, $p < 0.05$), significantly more subcaudals ($t = 4.760$, df = 18, $p < 0.001$), and greater relative tail lengths. Females attain a greater body size than males. The five largest females were 681–771 mm total length (541–595 mm SVL), and four of these were >700 mm total length. The five largest males were 568–657+ mm total length (422–520 mm SVL) and three of these were >600 mm total length. Large females appear to have somewhat different body proportions than smaller individuals of either sex, but larger samples of well-preserved specimens would be needed to test this observation rigorously. Additionally, because localities for *S. petersi* are represented by few individuals (most frequently one or two specimens per locality), it is difficult to separate divergence in characters because of sex from geographic or other sources of variation. Nonetheless, large females tend to have rather narrow, elongate heads and relatively small eyes; smaller individuals have shorter, more rounded, bulbous heads and larger eyes. Large females have rather stout bodies, especially posteriorly, compared with males (this comparison ignores the two females that were clearly carrying eggs).

Sex differences in head size and shape and body size and shape, such as those apparent in *Sibynomorphus petersi*, are relatively common in snakes (reviews in Bonnet et al., 1997; Shine, 1989, 1993). The head shape differences most often reflect intersexual dietary differences (e.g., Camilleri and Shine, 1990), whereas body shape differences, in which females have a stouter, robust body, most likely reflect the reproductive needs of female snakes to accommodate eggs or fat body stores (Lourdais et al., 2006).

Corresponding to the relatively longer SVLs of females compared with males, there is sexual dimorphism in the number of crossbands on the body. Females averaged 38 ± 8.01 bands on the body (range: 31–59, $N = 12$; ignoring a clear outlier at 59, the range is 31–44 with a mean of 36.0 ± 4.74). Males averaged 31.2 ± 1.69 bands (range: 29–35; $N = 10$). The overall means are significantly different (unequal variances, $t'_s = 2.949$, $t'_{0.05} = 2.203$, $p < 0.05$), as well as the comparison ignoring the female outlier (unequal variances, $t'_s = 3.049$, $t'_{0.02} = 2.77$, $0.01 < p < 0.02$).

Superimposed on this pattern of sexual dimorphism is geographic variation in the number of crossbands (Peruvian specimens tend to have greater numbers of crossbands; see below), but even considering only Ecuadorian specimens, females average about four more bands on the body than males.

Geographic Variation. Notable geographic trends in scutellation or body proportions are few in *Sibynomorphus petersi*, as shown for ventrals, subcaudals, and relative tail lengths in Table 4. None of these characters show statistically significant differences between Ecuadorian and Peruvian samples when sexes are compared separately. Three of six Peruvian specimens have a single anterior temporal on each side (the others have two), whereas all Ecuadorian specimens have either two or three anterior temporals. No other scutellation differences among Ecuadorian and Peruvian specimens were noted. Perhaps significantly, the only specimen of *S. petersi* from the Amazonian versant, MUSM-JEC 12884, has the lowest ventral count (164) of all specimens (range in the rest of the sample: 170–188; $N = 23$). No other characters of this specimen were unusual (unfortunately, it is a badly damaged road kill).

In addition to the sexual differences indicated above, the number of body crossbands varies geographically, but sample sizes are too small to thoroughly analyze the trend. The only Peruvian male with a full complement of crossbands has 35 bands on the body, whereas the range among Ecuadorian males was 29–32. Three Peruvian females had 41, 44, and 59 crossbands, whereas the range among Ecuadorian females was 31–38 and one outlier at 43. Thus, it seems likely that for

TABLE 4. GEOGRAPHIC COMPARISON OF SELECTED CHARACTERS IN *SIBYNOMORPHUS PETERSI*. THE TWO MALES FROM PERU HAD BROKEN TAILS, SO NO SUMMARY STATISTICS ARE AVAILABLE FOR SUBCAUDALS AND RELATIVE TAIL LENGTHS FOR MALES FROM PERU. NONE OF THESE CHARACTERS SHOW STATISTICALLY SIGNIFICANT DIFFERENCES BETWEEN ECUADORIAN AND PERUVIAN SAMPLES IN SEPARATE COMPARISONS BY SEX..

	Ecuador	Peru	Total Sample
Ventrals			
Male	170–183 174.3 ± 4.85 (N = 9)	164–176 170.0 ± 8.48 (N = 2)	164–183 173.5 ± 5.39 (N = 11)
Female	173–188 178.8 ± 5.06 (N = 8)	174–182 178.2 ± 3.35 (N = 5)	173–188 178.5 ± 4.33 (N = 13)
Subcaudals			
Male	75–87 81.0 ± 3.66 (N = 8)	65+ to 74+ (N = 2)	75–87 81.0 ± 3.66 (N = 8)
Female	65–77 73.3 ± 4.43 (N = 8)	70–74 72.5 ± 1.91 (N = 4)	65–77 73.0 ± 3.69 (N = 12)
Tail length/total length			
Male	0.22–0.28 0.25 ± 0.02 (N = 8)	0.21+ to 0.26+ (N = 2)	0.22–0.28 0.25 ± 0.02 (N = 8)
Female	0.20–0.24 0.22 ± 0.01 (N = 7)	0.20–0.24 0.22 ± 0.02 (N = 4)	0.20–0.24 0.22 ± 0.01 (N = 11)

both sexes, northern specimens tend to have fewer crossbands than southern ones.

Color in Life. The color pattern of *Sibynomorphus petersi* in life consists of various shades of brown (yellowish brown to dark brown) or gray. The dorsum is usually distinctly crossbanded, but three individuals from Peru have very indistinct crossbands. Bands are characteristically narrow and undulating or zigzag. The venter is heavily marked with bold spots, and the top of the head has complex dark markings, including the consistent presence of a large spot on each prefrontal (details below). The following color notes are available for individual specimens:

FMNH 232569 (Fig. 16 female, Río Zaña Study Site, 494 mm SVL): Dorsum medium rich brown with dark brown markings: a middorsal series of irregular spots and a lateral series forming oblique incomplete crossbands. Dorsal ground color lighter anteriorly than posteriorly. Head medium rich brown with dark irregular spots and markings on most scales. Gular region cream with dark brown peppering on lower labials (upper labials also have this peppering but the ground color is darker). Venter whitish anteriorly with large dark spots forming irregular, roughly parallel, series of broken lines on each side. Entire venter peppered with dark brown, which becomes denser posteriorly. Ventral surface of tail also peppered with dark brown. (Field notes of J. E. Cadle)

KU 121309 (Fig. 17. male, southern Ecuador, 351 mm SVL): Ground color medium brown extending to bottom of lower scale row; dorsum spotted and barred with darker brown, often edged with black; top of head medium brown with black spots; upper labials gray brown; chin white and dark brown; iris gray at top and bottom with broad brown band through it; tip of tongue black, remainder red. (Field notes of John D. Lynch)

KU 142804 (Fig. 18. male, southern Ecuador, 377 mm SVL): Dorsum brown with darker brown crossbars faintly outlined with creamy tan. Venter creamy white with black spots. Iris tan. (Field notes of William E. Duellman)

LSUMZ 27374 (male, northern Peru, 520 mm SVL): Dorsal ground color gray, markings black or very dark gray (gray-brown). Light flecking and isolated scales on edges of bands white. Venter paler gray with black spots and white spots, more extensive anteriorly. (Field notes of Richard Thomas for RT 3059)

Color in Preservative and Variation in Pattern. In preservative, the pattern elements (crossbands, head markings, ventral markings) remain distinct. In preserved specimens that have not lost the stratum corneum, the ground colors, crossbands, and other markings retain their brown color tones, although they are duller than in

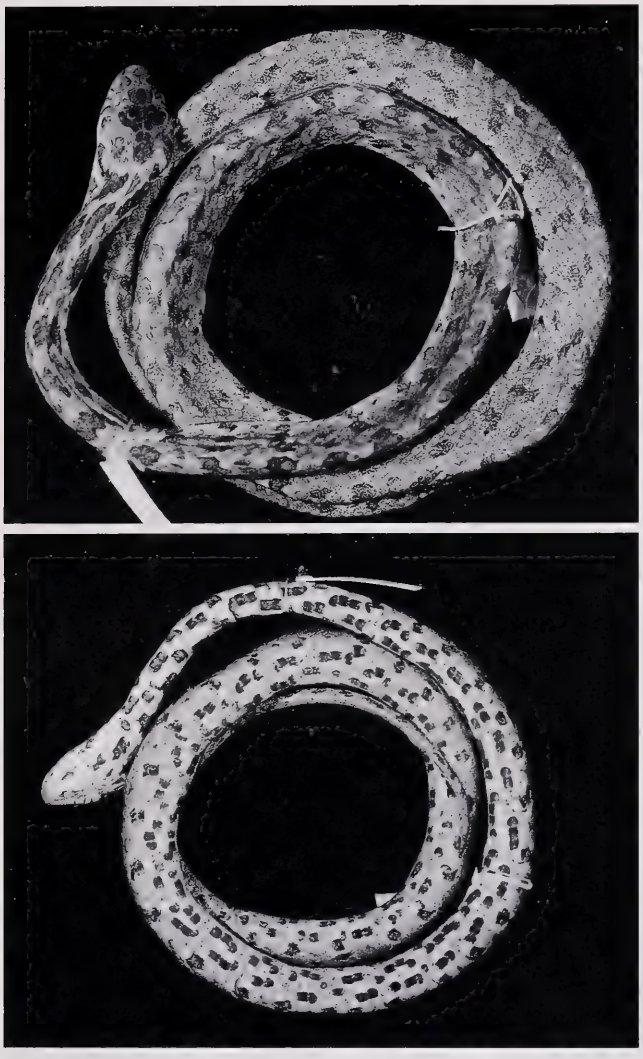


Figure 16. *Sibynomorphus petersi.* Dorsal and ventral views of FMNH 232569 (Río Zaña Study Site, Cajamarca Department, Peru). Female, 494 mm SVL. The crossbands in this specimen are fragmented into a series of irregular vertebral and lateral spots.

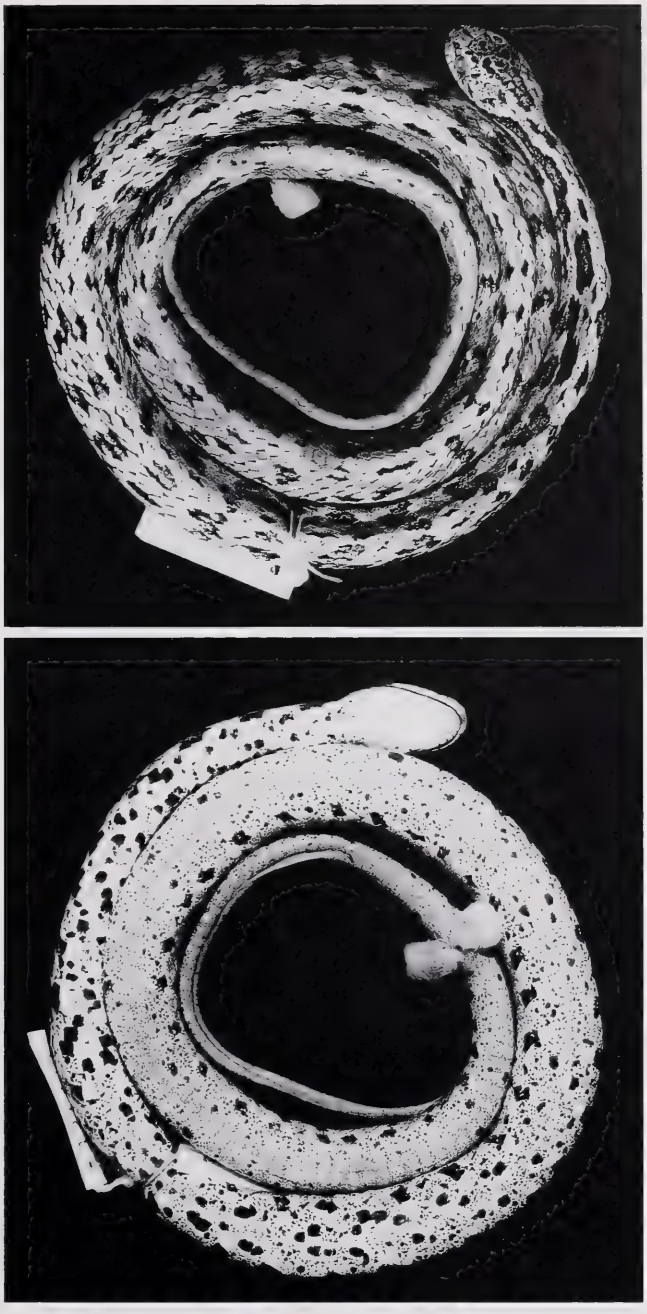


Figure 17. *Sibynomorphus petersi.* Dorsal and ventral views of KU 121309 (Loja Province, Ecuador). Male, 351 mm SVL.

life. With loss of the stratum corneum, the brown tones present in life are gray (in some older specimens, the ground color of such specimens is ash white). There is both sexual dimorphism and geographic variation in the number of crossbands on the body, as covered in previous sections.

Most specimens of *Sibynomorphus petersi* have a series of narrow zigzag or wavy crossbands that are complete across the dorsum (i.e., not alternating side to side). These crossbands usually have a very narrow light border and jagged edges (Fig. 14). A band on the nape and the following two to four crossbands are usually, but not always, broader than the others (Fig. 14). These anterior crossbands are sometimes incomplete across the vertebral line. Crossbands on the neck are occasionally absent and replaced by a broad longitudinal streak on each side (Fig. 18). In some individuals, the crossbands are fragmented laterally into a series of spots that can maintain the appearance of crossbands or are so fragmented that individual bands

Figure 18. *Sibynomorphus petersi.* KU 142804 (Loja Province, Ecuador). Male, 377 mm SVL. The dark streak on the side of the neck is characteristic of many specimens of *S. petersi.*

are difficult to discern, as described for three Peruvian specimens below.

The top of the head in *Sibynomorphus petersi* is brown or grayish brown with dark brown markings. A large discrete spot is present on each prefrontal (Fig. 19); although it varies in size, position, and shape, it is a constant feature of the pattern. Despite the variation in form, the prefrontal spots are sufficiently diagnostic of this species that specimens that otherwise differ greatly in pattern retain this character (compare Figs. 15, 19, 22, and the photos of corresponding dorsal patterns). Other large spots or reticulations are present on the frontal, parietals, and supraoculars; these can fuse with one another to form larger patterns (Fig. 19, lower right). In virtually all cases, the dark head markings have a narrow pale edge.

The venter has a whitish ground color with bold black or dark brown squarish or half-moon–shaped spots. These spots vary

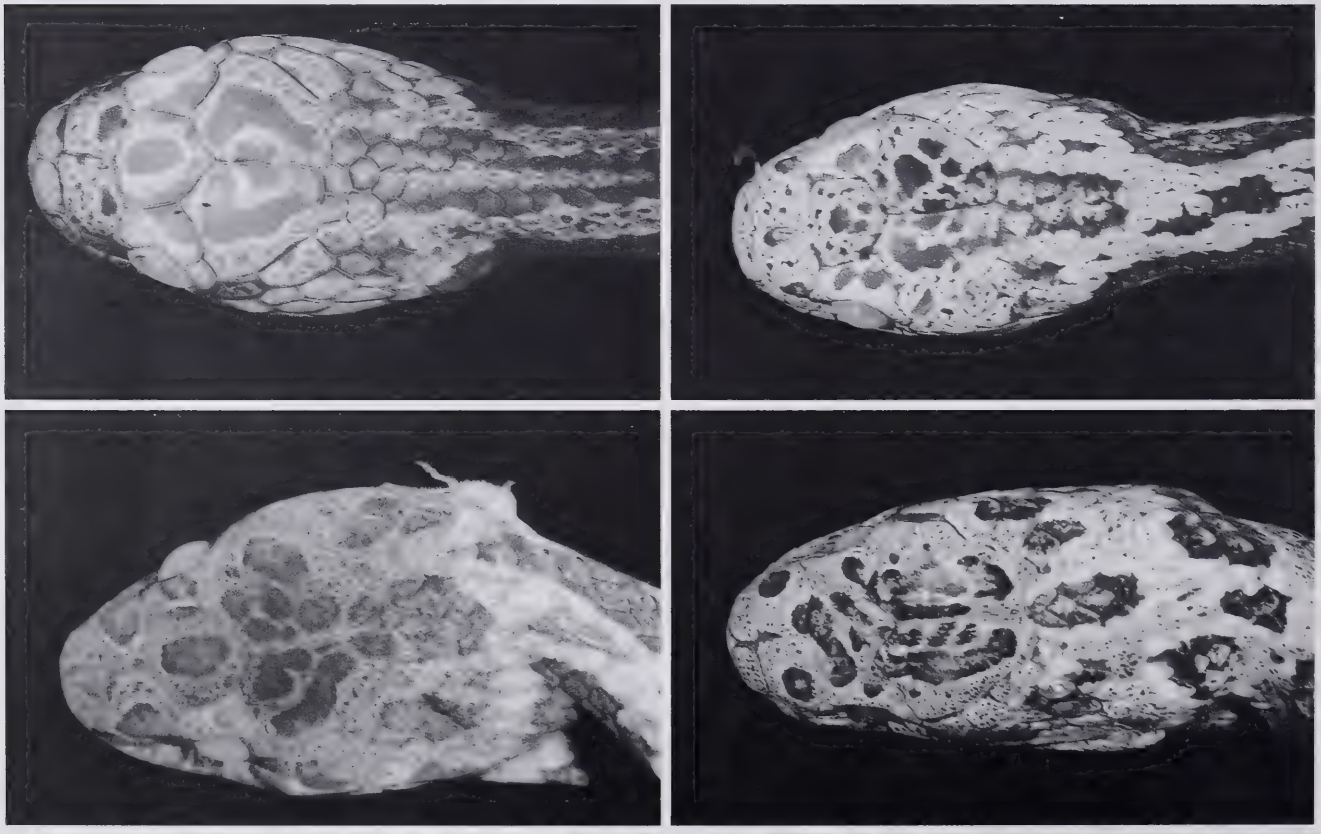


Figure 19. *Sibynomorphus petersi.* Dorsal views of heads. Top: left, KU 142804; right, KU 121309; both from Loja Province, Ecuador. Bottom: left, FMNH 232569; right, BMNH 1900.3.30.19; both from Cajamarca Department, Peru. These specimens show the characteristic prefrontal spots in *S. petersi* and some of the variation in the size, shape, and position of the spots.

in density, from series arrayed at the lateral edges of each ventral plate (Fig. 14) to denser arrays all across the venter and occasionally arrayed into larger patterns of streaks (e.g., Figs. 13, 16). The venter is often heavily peppered with fine dark brown. The dorsal bands do not encroach onto the ventral plates or encroach only to their extreme lateral edges.

Individual scales in *Sibynomorphus petersi* are typically finely flecked with minute dark brown spots, which are best seen under magnification. These spots seemingly appear on any scales of the body (dorsal and ventral) or head, with some variation in their density among specimens. Figure 15 (top) shows the pattern on head scales particularly well; for some of the variation, see Figures 17 (bottom), 19, 22, and 23.

Three Peruvian specimens, SMF 80048 (Fig. 20), FMNH 232569 (Fig. 16), and stomach contents associated with a *Micrurus mertensi,* ANSP 31806 (see Fig. 26), lack discrete crossbands over most or all of the body. In FMNH 232569 and ANSP 31806, a series of vertebral spots marks the position of the crossbands, and indistinct lateral bars are visible when the specimens are submerged in alcohol in good light. These unbanded specimens otherwise retain characteristic pattern elements of this species, as elaborated below. Other Peruvian specimens are banded with some variation: bold bands present the whole length of the body and tail (e.g., Fig. 21) to specimens with narrow, somewhat fragmented bands (e.g., Fig. 27).

The color pattern in preservative of SMF 80048 (Figs. 20, 22), one of two southernmost specimens of *Sibynomorphus petersi* known and one of three unbanded specimens, is as follows: Dorsal pattern indistinct, with no discrete bands. Ground color (dorsally, ventrally, and on head scales) brown, each scale on all of these areas finely speckled with minute dark brown specks. A large round dark brown spot on each prefrontal positioned toward the midline (Fig. 22). A similar, but more smudged spot on the anterior end of each parietal, more smudged on the right than on the left side. Dark suture lines to many dorsal scales give the appearance of irregular flecking on the dorsum. Posteriorly these dark edges tend to align into diagonal lines, but anteriorly they are more irregular. Nowhere are there regular lines or bands. The gular region is yellowish and unpatterned except for a very few minute flecks. The venter is heavily marked with irregular to half-moon–shaped dark brown spots, more or less aligned into irregular rows. In addition, very fine dark flecks cover the venter. The ground color of the venter is paler and more yellowish brown than the dorsum (medium brown).

The smallest specimen examined (USNM 237040 from southern Ecuador, 184 mm SVL) still has an unfused umbilical scar. It has irregular crossbands over the dorsum similar to some adult patterns and otherwise does not differ substantially from the color pattern of adults. Thus, there is little or no ontogenetic change in color pattern.

To summarize, several features of the color pattern of *Sibynomorphus petersi* are relatively constant and are helpful in identifying this species: (1) Narrow zigzag crossbands with irregular edges, and often a longitudinal lateral neck bar. (2) A spot, usually rounded and of varying size and position, on each prefrontal scale. These spots are sometimes positioned toward the midline near the suture between the prefrontals and sometimes more laterally; they are usually on the posterior half of the prefrontals (Figs. 15, 19, 22, 23). Like other markings on top of the head, these spots are often surrounded by a narrow pale border. Even in specimens that otherwise differ greatly in pattern, including those lacking definitive crossbands on the dorsum, these spots are invariably present (Fig. 22). (3) Minute dark brown speckling on individual dorsal and ventral scales (e.g., Fig. 15, top). In specimens with less distinct dorsal bands, the bands are usually

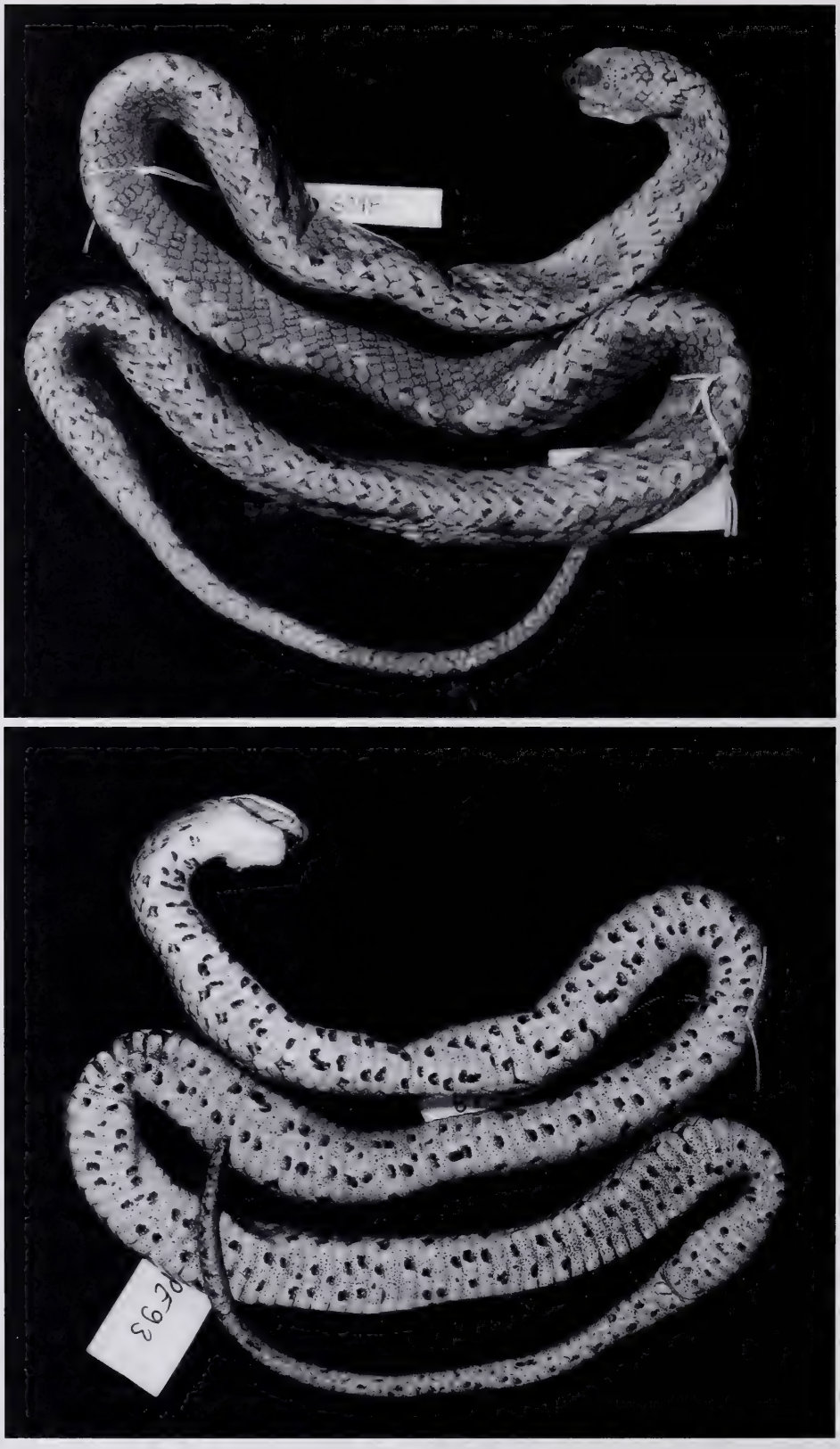


Figure 20. *Sibynomorphus petersi.* Dorsal and ventral views of SMF 80048 (Ancash Department, Peru). Female, 492 mm SVL. This is one of two southernmost specimens of *S. petersi* known. The specimen entirely lacks discrete crossbands, instead having a dorsal pattern of fine streaks and reticulations.

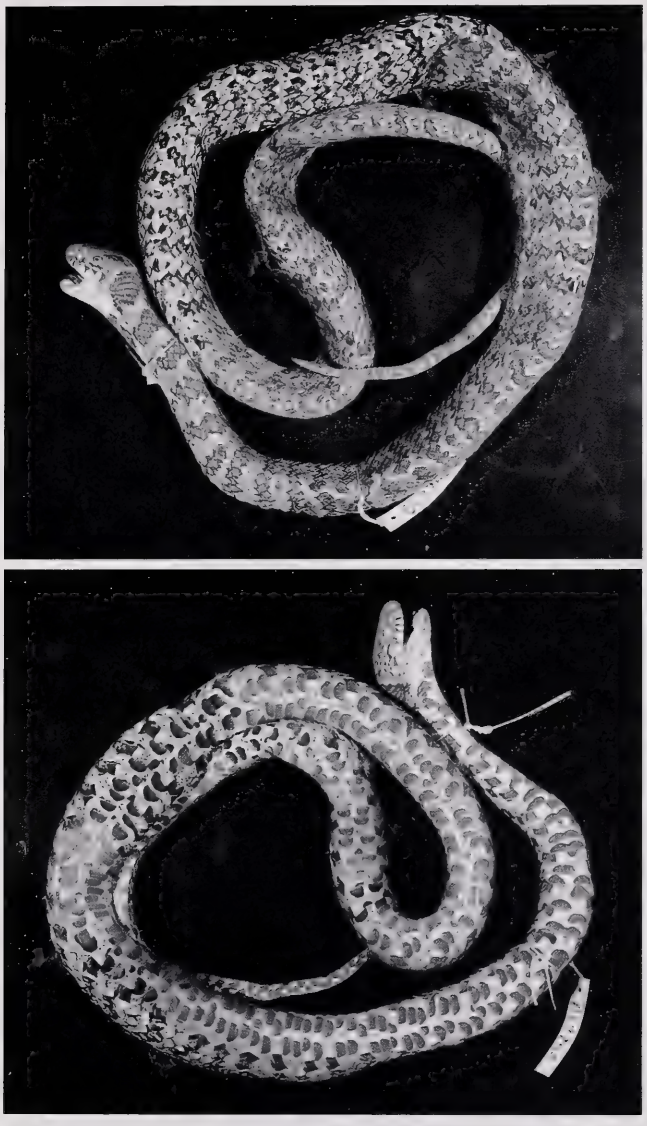


Figure 21. *Sibynomorphus petersi.* Dorsal and ventral views of MCZ 178047 (Bosque Cachil, Cajamarca Department, Peru). Female, 543 mm SVL. This specimen is more completely banded than most specimens of *S. petersi.*

Figure 22. *Sibynomorphus petersi* from Ancash Department, Peru. Dorsal view of head (SMF 80048). The head is relatively unpatterned compared with most *S. petersi* (compare Figs. 19, 23) but still retains the characteristic prefrontal spots.

Figure 23. *Sibynomorphus petersi.* Dorsal and lateral views of head (MCZ 178047). The prefrontal spots in this specimen are exceptionally large and show the surrounding pale ring particularly well. Also visible are the minute dark specks that pepper individual scales on most specimens of *S. petersi* (especially visible on the posterior dorsal head scales and lateral scales around the jaw angle).

indicated as a discrete increase in the density of this characteristic dark peppering. (4) The venter is heavily marked with bold half-moons or squarish spots (Fig. 21), often in longitudinal arrays. In addition, the venter is often heavily invested with fine dark brown minute spots.

Etymology. Sibynomorphus petersi was named for James A. Peters, former curator in the Division of Amphibians and Reptiles at the National Museum of Natural History.

Hemipenis

Field-everted hemipenes were available for two specimens of *Sibynomorphus petersi*: KU 142804 (Loja Province, Ecuador) and LSUMZ 27374 (Piura Department, Peru). These organs are virtually identical and the following detailed description is based on KU 142804.

The hemipenis of KU 142804 is nonbilobed (single) and fully capitate (Fig. 24).

Figure 24. Hemipenis of *Sibynomorphus petersi* in sulcate view (KU 142804).

Total length of the organ is approximately 13 mm. Length of the capitulum on the sulcate side approximately 7 mm. The sulcus spermaticus divides within the capitulum and has more or less centrolineal branches, but each branch ultimately passes somewhat laterally to end at the outer (lateral) periphery of the tip of the organ. Proximally, the hemipenis has minute spines all over, although these are sparse, especially on the asulcate side. A battery comprising about three rows of enlarged hooked spines completely encircles the midsection of the organ just proximal to the capitulum. These spines are larger adjacent to the sulcus spermaticus than on the asulcate side.

The capitulum is completely ornamented with papillate calyces. Calyces are well developed, but proximally, the longitudinal connections between them tend to break down so as to give the appearance of weakly developed, but densely arrayed, flounces. The calyces are surmounted by large blunt papillae. Because the proximal calyces tend to be poorly formed, there is the appearance of about three rows of papillae (or papillate flounces) encircling the base of the capitulum. Probing with a fine needle suggests that these proximal papillae might be somewhat mineralized.

A very large nude pocket (3.5 mm long) is present on the lateral side of the organ (i.e., midway between the sulcate and asulcate surfaces); it extends from the very base of the organ to the battery of spines on the midsection. The pocket has thickened borders, which are especially prominent at the middle of the pocket. A small, but distinct, fleshy lobe is present on the asulcate side of the pocket slightly more distal than its midpoint. Distally, the pocket is bordered by two large hooked spines on one side and a similar spine on the other. These spines are larger than any of those in the midsection battery and are positioned at the proximal border of the battery. In LSUMZ 27374, the spines at the distal edge of the nude pocket are not as closely associated with the pocket as in KU 142804. In particular, the large pair of spines on the asulcate edge of the nude pocket could be viewed in either specimen as having no special association with the nude pocket.

Distribution and Natural History

Sibynomorphus petersi is known from southwestern Ecuador (Azuay and Loja Provinces) and northern Peru south to southern Ancash Department (10°09′S) (Fig. 25; see also Fig. 43). The Ecuadorian localities and all Peruvian localities except one are on the Pacific versant of the Andes. MUSM-JEC 12884 documents that the species also occurs east of the continental divide in the Río Chotano drainage, which flows northward and joins the Río Huancabamba to form the Río Chamaya, a western affluent of the Río Marañón. The documented elevational range is 1,457–2,250 m for Ecuadorian localities and 1,250–3,120 m for Peruvian localities.

Two specimens of *Sibynomorphus petersi* were obtained at the Río Zaña Study Site (Cajamarca Department, Peru). FMNH 232569 was found at midmorning recently killed on a trail through secondary growth (brushy hillsides, agricultural land) on 2 May 1987 (early dry season). The freshness of the specimen on a hot day suggests that it might have been active during the day when killed. Another spec-

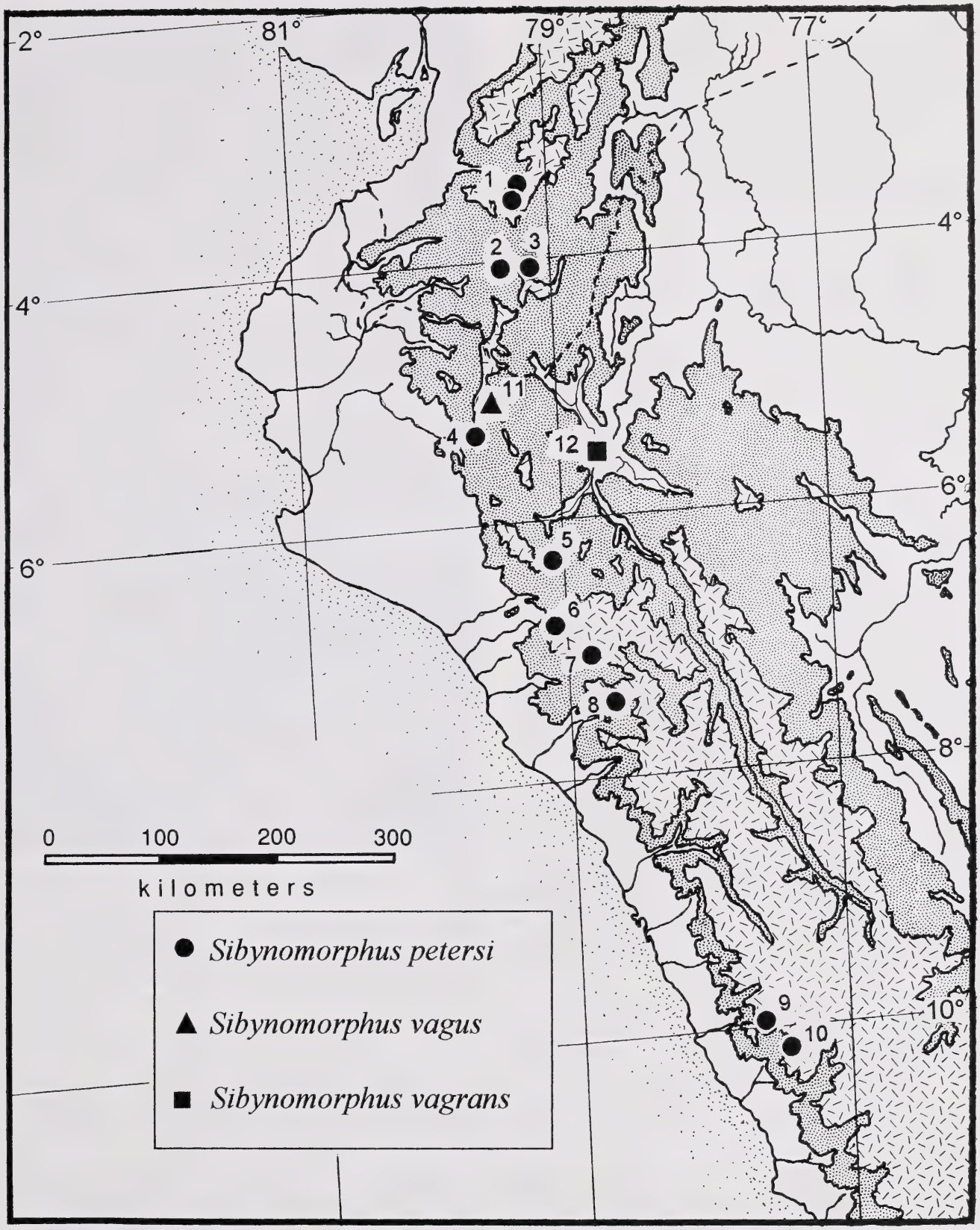


Figure 25. Distributions of *Sibynomorphus petersi, S. vagrans,* and *S. vagus* in southern Ecuador and northwestern Peru. All known localities are plotted (locality 3 represents multiple contiguous localities). See Figure 43 for amplification of the southern portion of the distribution of *S. petersi* (Ancash Department, Peru). Stippled area is above 1,000 m; hatched area is above 3,000 m. Numbers are locality records, as follows: ***Sibynomorphus petersi***: *Ecuador*: (1) Zhila (type locality, north) and El Tablón (south); (2) Río Catamayo valley; (3) Loja city and vicinity (multiple localities); *Peru*: (4) Canchaque; (5) Paraguay, Río Chotano (Amazonian versant); (6) Río Zaña Study Site; (7) San Pablo; (8) Bosque Cachil; (9) Malvas; (10) Cajacay. ***Sibynomorphus vagus***: *Peru*: (11) Huancabamba. ***Sibynomorphus vagrans***: *Peru*: (12) Bellavista.

imen from the Río Zaña Study Site had been swallowed head first by a *Micrurus mertensi,* ANSP 31806 (Fig. 26). The *Micrurus* is 573 mm SVL (total length 652 mm) and the *Sibynomorphus* (not separately catalogued) is approximately 465 mm SVL (total length 613 mm); the specimen was collected by a local resident in early November 1988 (late dry season/ transition to rainy season).[11] MCZ 178047 was collected 12 October 1992 at Bosque Cachil at the edge of the humid forest; Cadle and Chuna (1995) and Sagástegui et al. ("2003" [2004]) describe this forest.

MUSM-JEC 12884, a road kill in poor condition, was collected 10 August 1994 near Paraguay in the Río Chotano valley (Cajamarca Department, Peru) and is the only specimen from the Amazonian versant (Fig. 25). This area once harbored extensive montane humid forests, but by 1994, these forests had been reduced to scattered patches, mainly on steep hillsides and in riparian strips. Otherwise, pasture and agricultural land were extensive. The area was dissected by rocky streams with occasional waterfalls. My field notes described the forest as "rich tropical montane humid forest with abundant tree ferns and large bromeliads. Canopy 20–30 m high, with some palms. Abundant epiphytes with a diversity of orchids. Secondary growth forest on some steep hillsides in areas of former landslides." MUSM-JEC 12884 was collected in a deforested area.

Ancillary field data accompany a few other specimens of *Sibynomorphus petersi.* KU 142804 was collected 23 July 1971 at the base of an agave plant growing on a mud fence by day. KU 121309 was collected 12 June 1968 underneath a rock buried in soil along the edge of a stream. LSUMZ 27374 was found 1 December 1974 by day under a log in a partly overgrown pasture (Richard Thomas, field notes). SMF 80048 was collected 2 February 1997 under a rock exposed to the sun (Lehr et al., 2002: 383).

The first specimen of *Sibynomorphus petersi* to make its way into collections from Peru is BMNH 1900.3.30.19 (Figs. 15, 19, 27), collected at San Pablo, Caja-

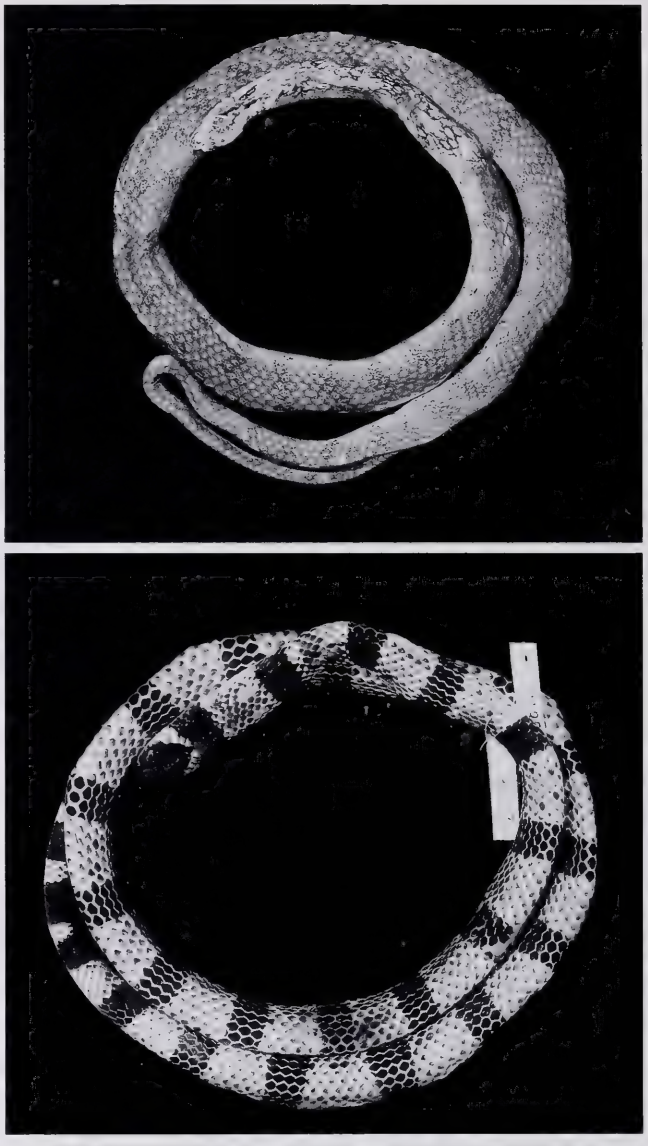


Figure 26. Prey and predator: *Sibynomorphus petersi* (top) from the stomach of *Micrurus mertensi* (bottom; ANSP 31806). Both photos are to the same scale. Approximate total length of the *Sibynomorphus* is 613 mm. Total length of the *Micrurus* is 644 mm. The dorsal crossbands in the *Sibynomorphus* were visible only under alcohol and in good light.

[11] The *Sibynomorphus* is intact except that scales covering the head and approximately the anterior 25–30 mm of the body are digested away. The specimen has very indistinct crossbands and the diagnostic aspects of head pattern could not be evaluated. Ventral counts and body measurements were determinable within narrow limits because the exposed vertebral column and skull were still intact; however, no head scales remained.

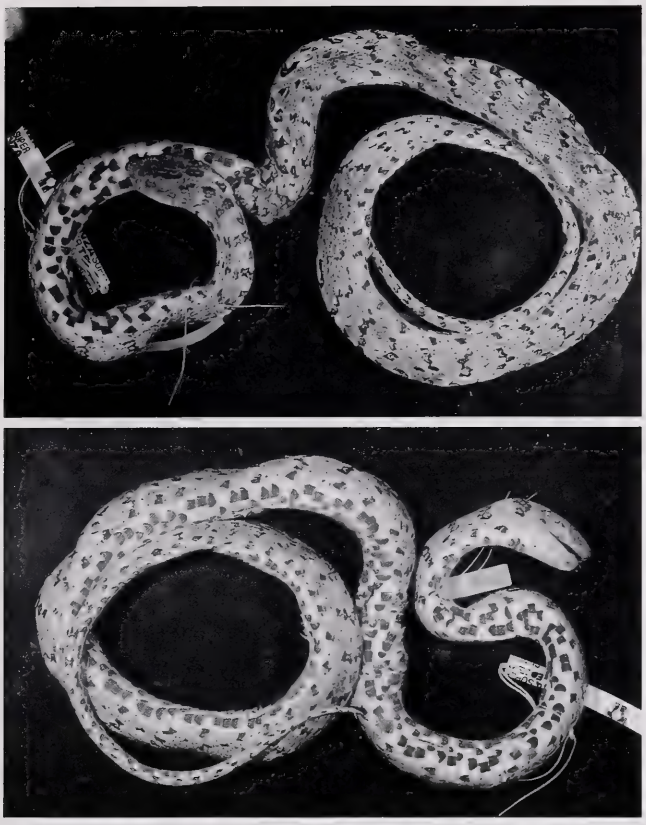


Figure 27. *Sibynomorphus petersi.* Dorsal and ventral views of BMNH 1900.3.30.19 (San Pablo, Cajamarca Department, Peru). Female, 595 mm SVL.

marca Department by Perry O. Simons on 5 November 1899 (the date comes from Simons' itinerary published by Chubb, 1919; see Cadle, 1998: footnote 6). Simons' South American herpetological collections were described by Boulenger (1899, 1900, 1901, 1902a,b), but he mentions no snakes other than *Philodryas simonsii, Homalocranium marcapatae* (= *Oxyrhopus marcapatae*), and two species of *Elaps*: *E. simonsii* (= *Micrurus pyrrhocryptus*) and *E. regularis* (= *M. annellatus*). I visited San Pablo and vicinity 16–17 August 1994, and my field notes indicate that "all natural habitat in the broader area has been destroyed—now only agricultural land, secondary forest, and some brushy vegetation along fence rows . . . few streams. . . . Vegetation included much *Eucalyptus* and *Opuntia* as well as cultivated agaves. Terrain [was] very steep and at this time very dry."

Two females from southern Ecuador (BMNH 1924.6.24.110, 550 mm SVL, 720 mm total length; BMNH 1933.6.24.110, 541 mm SVL, 711 mm total length), dates of collection unknown, each contained five large eggs (determined by palpation). The smallest specimen examined (USNM 237040, 184 mm SVL) still has an unfused umbilical scar and was collected 2 August 1954.

The region of southern Ecuador and northern Peru from which *Sibynomorphus petersi* is known has a complex topography and, consequently, a diversity of environments, including relatively arid inter-Andean valleys (e.g., Río Catamayo) and humid forests on the Andean slopes (Chapman, 1926). Few specific data are available for the ecological distribution of *S. petersi* within this region, although some localities (e.g., the Río Catamayo valley of southern Ecuador and the slopes of the Andes in southern Ancash Department, Peru) are relatively more arid than others (e.g., Río Zaña Study Site and the single known locality on the Amazonian versant). Orcés and Almendáriz (1989: 59) reported the following concerning the Ecuadorian localities for *S. petersi* (see also the species account for *S. oligozonatus*):

> The places . . . ecologically correspond to the life zone of Lower Montane Dry Forest . . . that Chapman called Arid Temperate. Annually, rainfall reaches 500 to 1000 mm. Geographically, to this zone belong the dry plains and canyons of the inter-Andean valleys (toward the interior basins), at altitudes between 2000 and 3000 m above sea level, in the edges of the Lower Montane spiny steppes and Lower Montane humid forest. The natural vegetation . . . has been replaced by cultivated land and there remain few areas covered by *algarrobos.*

In Peru, several localities for *Sibynomorphus petersi* are associated with remnants of humid forests occupying the western Andean slopes or (one specimen) the more humid eastern slopes. Three localities (Canchaque, Río Zaña Study Site [= Bosque Monteseco], and Cachil) are among the best studied and most diverse humid forests on the western slopes of the Andes in Peru (Dillon et al., 1995; Sagás-

tegui et al., "2003" [2004]). Although these are humid forests (with abundant epiphytes and other indicators), the region experiences a pronounced dry season as well. Cadle and McDiarmid (1990: 765–766) and Cadle (2005: 70–71) gave general descriptions and climatic regimes of the Río Zaña Study Site, and Cadle and Chuna (1995: 21–24) described Bosque Cachil.

The two specimens of *Sibynomorphus petersi* from the Río Zaña Study Site are from an area of transition (1,250–1,400 m) between the humid forests on the slopes (above about 1,500 m) and the dry forest characteristic of lower elevations (<1,000 m). Whether *S. petersi* occurs at lower elevations within the dry forest zone is unknown. Despite intensive sampling within humid forests between 1,500 and 2,500 m at the Río Zaña Study Site,[12] the species was not obtained at these elevations, suggesting that it might be more characteristic of the transition zone or the dry forest itself. The three specimens from the Río Zaña Study Site and Bosque Cachil were collected in the early and late dry season (May, October, November). The only specimen from the Amazonian versant, MUSM-JEC 12884, was collected 10 August 1994; the Amazonian versant is more continually humid than the Pacific versant.

A specimen collected by Richard Thomas (LSUMZ 27374) was obtained as part of faunal studies undertaken by the LSUMZ beginning in 1974, when Thomas and Theodore A. Parker III established a camp near the summit of the Cordillera de Huancabamba (3,050 m) and worked on the western slope of the cordillera in late November and early December (approximately the transition between the dry and rainy seasons). LSUMZ 27374 was collected at 2,073 m. Parker et al. (1985: 170), under the name "Cruz Blanca,"[13] described the general environment:

> The west slope was covered by a mixed evergreen forest (including *Clusia, Oreopanax, Podocarpus,* and *Polylepis*). . . . Human pressure on this habitat is increasing . . . and forest is being cleared from above and below. Only scattered patches of forest exist below 2150 m. A mule trail descends about 1000 m from Cruz Blanca through mature forest, continuing downward through cleared lands to Canchaque. We worked the forest along this trail almost daily during our visits. Treeline forest is dominated by *Polylepis,* with a canopy 4 to 6 m high. Taller trees cover the lower slopes and stream valleys. Arboreal bromeliads are conspicuous, but tree ferns are absent (or very scarce), and *Chusquea* bamboo is uncommon. . . . Foggy, cloudy weather occurred regularly on all three visits.

Lehr et al. (2002) characterized Malvas and Cajacay (Ancash Department; SMF 80048, MUSM 20583), two localities from which they obtained specimens, as "montane steppe." Their photograph (Lehr et al., 2002: fig. 10) of the environment at Malvas shows open, mountainous terrain with shrubs, agaves, and eucalyptus trees. Lehr et al. (2002) described montane steppe as having "an arid climate with increases in precipitation and decrease in temperature during the [austral] summer. . . . The vegetation is sparse and forest negligible in extent."

Sibynomorphus petersi is sympatric with *S. oligozonatus* in southwestern Ecuador (see account for *S. oligozonatus*). *Sibynomorphus petersi* is also broadly sympatric with another dipsadine, *Dipsas oreas,* and the two species' geographic ranges are very similar (Fig. 25; Cadle, 2005: fig. 23). *Sibynomorphus petersi* and *D. oreas* are known to be sympatric at two localities on the western slope of the Andes in northern Peru: the Río Zaña Study Site (Cajamarca Department) and between Canchaque and the summit of the Cordillera de Huancabamba (Piura Department). However, the

[12] Field work at the study site covered 55 days during the early dry season (May–June 1989) and 18 days during the rainy season (January 1991). A basecamp was established at 1,800 m within the humid forest and collections were made from about 1,000–3,000 m, with greater emphasis between 1,500 and 2,500 m.

[13] These forests are referred to under the name "Canchaque" or "Bosque Canchaque" in much of the floral and faunal literature on this area (e.g., Cadle, 1991; Dillon et al., 1995; Sagástegui et al., "2003" [2004]).

two species might be segregated by habitat, with *S. petersi* occurring in more mesic to arid habitats than *D. oreas* (see footnote 7).

Sibynomorphus vagrans (Dunn) Figures 28–32

Pseudopareas vagrans Dunn, 1923: 187. Type locality: "Bellavista [Cajamarca Department], Peru." Holotype, MCZ 17284.

Pseudopareas vagus vagrans: Amaral, "1929"a [1930]: 33; "1929"b [1930]: 201; "1929"c [1930]: 75.

Sibynomorphus vagrans: Peters, 1960: 161, pl. IVe; 1965: 13. Orcés and Almendáriz, 1989. Scrocchi et al., 1993. Carrillo de Espinoza and Icochea, 1995.

Sibynomorphus vagrans is known only from the type series collected by G. K. Noble, all from Bellavista and originally catalogued in the Museum of Comparative Zoology. Noble's series originally comprised the holotype and 26 paratypes, of which some were exchanged to other collections (see footnote 25). I am aware of one other specimen from a "Bellavista" whose reference to *S. vagrans* is highly questionable (MUSM 2258); it is discussed separately at the end of this species account and is not included in the diagnosis and description of *S. vagrans* presented here.

Notes on the Holotype of *Sibynomorphus vagrans*

The holotype of *Sibynomorphus vagrans* (MCZ 17284) is an adult female in good condition, 557 mm total length, 425 mm SVL. Tail (132 mm) 23% of total length. Dorsal scales in 15–15–15 rows, 156 ventrals, anal scale single, and 73 subcaudals. Preoculars 1/2, postoculars 2/2, temporals 1 + 2 + 3 on each side. Supralabials 10 with 4–6 touching the eye on the left, 8 with 4–5 touching the eye on the right. Infralabials 12/12. One pair of infralabials is in contact behind the mental and there are three pairs of polygonal chin shields.

Diagnosis

Sibynomorphus vagrans is a brownish or grayish snake with a variable number (5–10) of broad dark crossbands anteriorly, much wider than the interspaces, and a posterior pattern consisting of an obscure network-like pattern, irregular flecks, or narrow, somewhat indistinct, irregular crossbands (much narrower than interspaces) (Fig. 28). The venter is unmarked (most specimens) or has a few dark spots that never form dense arrays. This species has a relatively low number of ventrals (149–155 in males, 154–159 in females) and relatively high number of subcaudals (80–87 in males, 72–79 in females). The top of the head is ornately patterned and the nape has a narrow pale collar with a characteristic obtuse angular shape.

Sibynomorphus vagrans is distinguished from all other species of the genus in northern South America by its combination of relatively low ventral counts and high subcaudal counts (Table 1). *Sibynomorphus vagus* is similar to *S. vagrans* in ventral counts but lacks well-defined crossbands anteriorly (and they are narrower than interspaces when present), lacks a pale nape collar, and has fewer subcaudals (60–65 in males, 56–60 in females). In addition, *S. vagrans* has a longer tail on average (25–29% of total length in males, 23–26% of total length in females) than *S. vagus* (23–24% in males, 20–21% in females).

Distinct broad anterior crossbands similar to those of *S. vagrans* are found only in *S. oligozonatus* and *S. williamsi*. *Sibynomorphus oligozonatus* differs from *S. vagrans* in having a foreshortened snout (compare Fig. 4 and Figs. 30, 31), fewer subcaudals, and fewer supralabials (6–7 vs. 8–9 in *S. vagrans*). *Sibynomorphus williamsi* differs from *S. vagrans* in having 6 supralabials (3–4 touching the eye) compared with 8 (usually) with 4–5 touching the eye in *S. vagrans*, higher ventral counts (173–188), lower subcaudal counts (56–73), and in *S. williamsi*, the dorsal crossbands are distinct virtually the entire length of the body (sometimes dorsal saddles and alternating lateral blotches posteriorly). *Sibynomorphus oneilli* differs

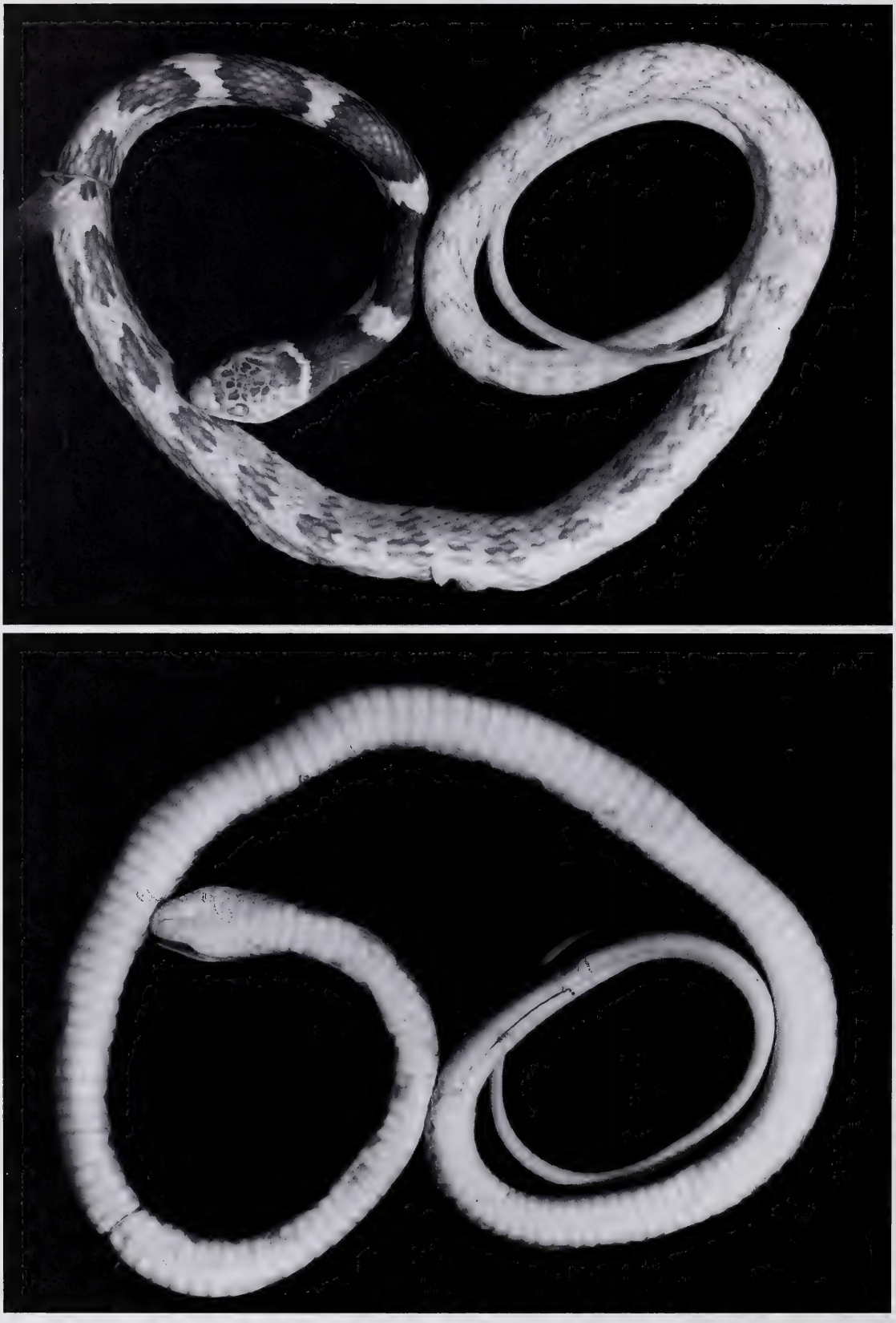


Figure 28. *Sibynomorphus vagrans* Paratype (MCZ 17439). Male, 387 mm SVL.

from *S. vagrans* in having more ventrals (≥152 in males, ≥160 in females), fewer subcaudals (62–77 in males, 57–64 in females), a shorter tail (22–26% of total length in males, 20–22% in females), a less ornately patterned head, narrower anterior dorsal crossbands, and a venter heavily marked with bold black spots. *Sibynomorphus petersi* differs from *S. vagrans* in having more ventrals (>160), a primarily brown dorsum with narrower crossbands (when present), interspaces brown (compared with whitish in *S. vagrans*), and a venter densely patterned with dark brown markings.

Description

Size and Scutellation. Descriptive data for *Sibynomorphus vagrans* are presented in Table 1. The largest specimen is the female holotype, 557 mm total length, 425 mm SVL. The largest male is 543 mm total length, 387 mm SVL. Tail 25–29% of total length in males, 23–26% of total length in females. Body moderately compressed. Dorsal scales smooth and in 15–15–15 rows. The vertebral row is not enlarged or only very subtly enlarged compared with paravertebral rows. Ventrals 149–155 (averaging 151) in males, 154–159 (averaging 157) in females (but see Table 1, footnote 2). Anal single. Subcaudals 80–87 (averaging 83) in males, 72–79 (averaging 74) in females. The loreal and a single preocular border the eye in most specimens (preocular superior to the loreal); the loreal is longer than tall. In three specimens, the loreal is vertically divided, resulting in a small triangular or trapezoidal preocular in addition to the usual one between the eye and the prefrontal scale. Postoculars 2 or, rarely, 3. Primary temporals usually 2 (occasionally 1 or 3). Secondary temporals 2 or 3. Tertiary temporals usually 3 (occasionally 4). Supralabials usually 8 (rarely 9 or 10) with 4–5 bordering the eye (rarely 4–6 or 3–5). Infralabials usually 11 or 12 (range 9–13). One pair of infralabials in contact behind the mental in all specimens ($N = 18$). Generally 3 pairs of chin shields (16 specimens); occasionally 2 pairs (2 specimens) or 2.5 pairs (1 specimen). Maxillary teeth 15–17 ($N = 9$). The pupil is prolate (Myers, 1984) in preserved specimens.

Peters (1960: 162–163), who examined five specimens not seen in this study (see footnote 25), noted individual variations in scutellation within *Sibynomorphus vagrans* that were not observed in my sample. The only consequential difference between Peters' (1960) description and the one here is that Peters indicated the range of subcaudals for male *S. vagrans* as 74–87 (my data: 80–87). There are a few discrepancies between my description and Peters' (1960) on one hand, and the original description (Dunn, 1923: 187–188). Dunn reported a range in ventral counts (sexes combined) of 142–155, whereas Peters' count (149–160) and mine (149–159) are nearly identical. Dunn reported the maxillary tooth count as "about 12 equal teeth," whereas my counts for nine specimens were 15–17 and Peters' for 11 specimens were 14–18. Dunn reported that one specimen had a divided anal scale; this specimen is probably MCZ 17444, which has a partially divided anal plate.

Sibynomorphus vagrans exhibits typical patterns of sexual dimorphism for colubrids. In comparison to females, males have significantly fewer ventrals ($t = 6.692$, df = 17, $p < 0.0001$), significantly more subcaudals ($t = 7.892$, df = 17, $p < 0.0001$), and greater relative tail lengths (Table 1).

Color in Life. Unknown. Dunn (1923: 188) used the expression "belly yellow" in describing the holotype, which might reflect the ventral color still apparent when he described the species. The venter of the type series as of 2003 was grayish white.

Color in Preservative. The color pattern of *Sibynomorphus vagrans* is very consistent among the specimens examined. All specimens have a series of five to 10 broad, bold dark brown crossbands anteriorly that become narrower and increasingly frag-

Figure 29. *Sibynomorphus vagrans* Paratype (MCZ 17442). Male, 230 mm SVL.

mented posteriorly (Figs. 28, 29). The anterior crossbands are widest middorsally (generally spanning 5–9 middorsal scale rows) and narrower laterally (spanning 3–6 dorsal rows). The bands in some specimens have a distinctly darker brown narrow border (Figs. 28–30). Bands extend ventrally to the outer edge of the ventral scales. The first dorsal crossband is separated from the dark spotting on the top of the head by a distinct narrow (2 scales or less) whitish collar just posterior to the mouth commissure; the collar connects to the pale gular region on each side and forms a characteristic obtuse angle middorsally with the vertex directed posteriorly (Fig. 30). In MCZ 17447, the first crossband behind the head is interrupted middorsally and thus forms an elongated blotch on each side of the neck; the crossbands in other specimens are complete across the dorsum. The dorsal ground color is dull grayish brown. The venter of most specimens is immaculate (dull grayish or whitish), but some specimens have a variable amount of dark brown flecks or spots, especially concentrated toward the outer edges of the ventral scales.

The top of the head is ornately marked with irregular dark brown spots and blotches (Fig. 30). A consistent feature of the head pattern is a broad, irregular band extending across the posterior edge of the prefrontals, curving over the canthus, and extending ventrally to the top half of the loreal scale (Figs. 30, 31). This band is interrupted at the suture line between the prefrontals in some specimens (Fig. 30, lower left) and occasionally on the lateral portion of the prefrontals on one or both sides (Fig. 30, upper right). Nonetheless, it is a consistent feature of head pattern in all the specimens examined. The supralabial sutures are outlined with dark brown in all specimens and the same is true for the infralabial sutures in most specimens; in a few specimens, the sutures of the chin shields and other gular scales are also marked.

Three small juveniles (MCZ 17446, 17451–52; SVLs of 181, 163, and 147 mm, respectively) do not differ in color pattern from adults. MCZ 17451–52 still have obvious umbilical scars, so the pattern probably does not change ontogenetically.

Etymology. Dunn (1923: 187) did not elaborate on the meaning of his species epithet, saying only that *Sibynomorphus vagrans* was "a species closely allied to [*S. vagus*] but quite distinct." To reflect his supposition that the two species were closely related, Dunn might have used the name *vagrans* (originally of Anglo-French and Germanic origin) because it is a latinized cognate associated with the Latin word *vagus* (meaning wandering or roaming or indefinite; from *vagor,* to wander).

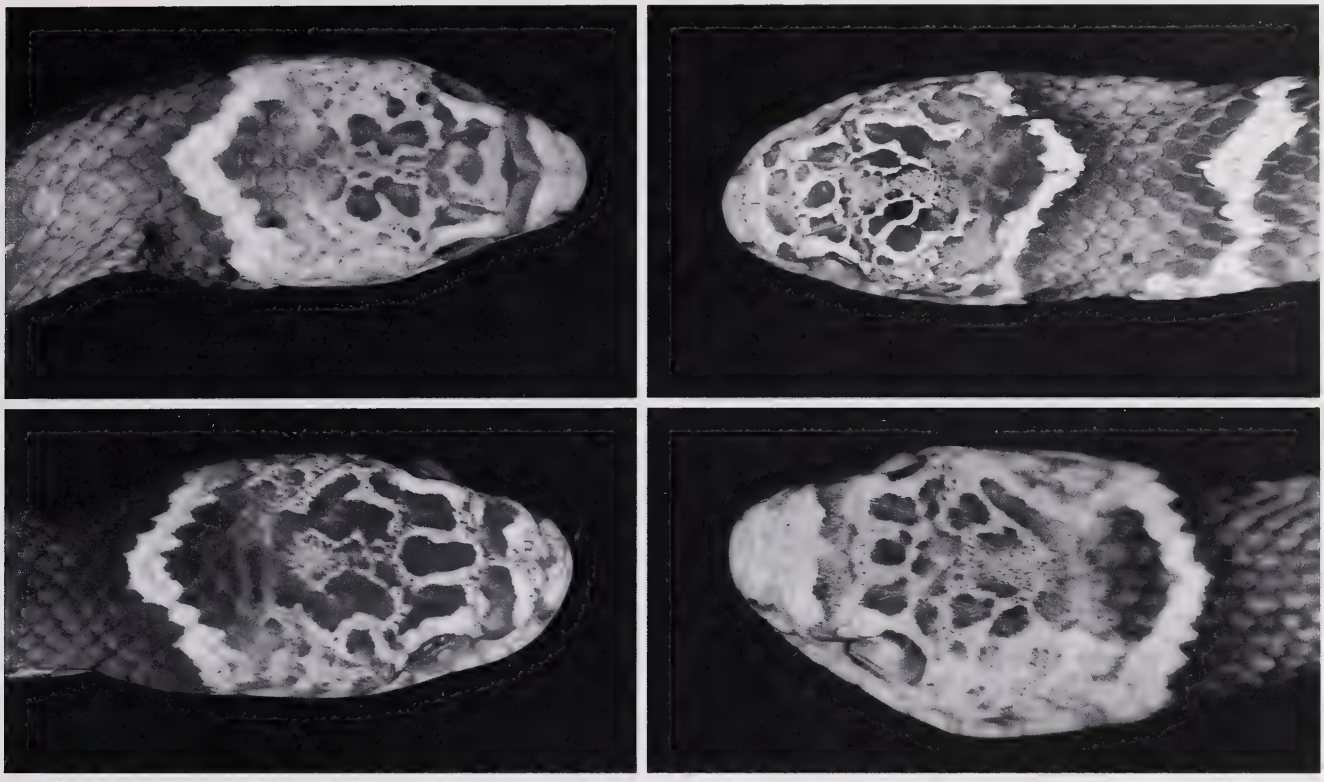


Figure 30. *Sibynomorphus vagrans.* Dorsal views of heads. Top: MCZ 17436 (left), MCZ 17440 (right). Bottom: MCZ 17442 (left), MCZ 17439 (right). These illustrate the ornate patterning atop the head of this species and two characteristic features of the pattern: an angular pale nape collar and a narrow dark band across the posterior portions of the prefrontal scales. The prefrontal band is complete in MCZ 17436 (top left) and shows varying degrees of interruption in the other three (see also Fig. 31).

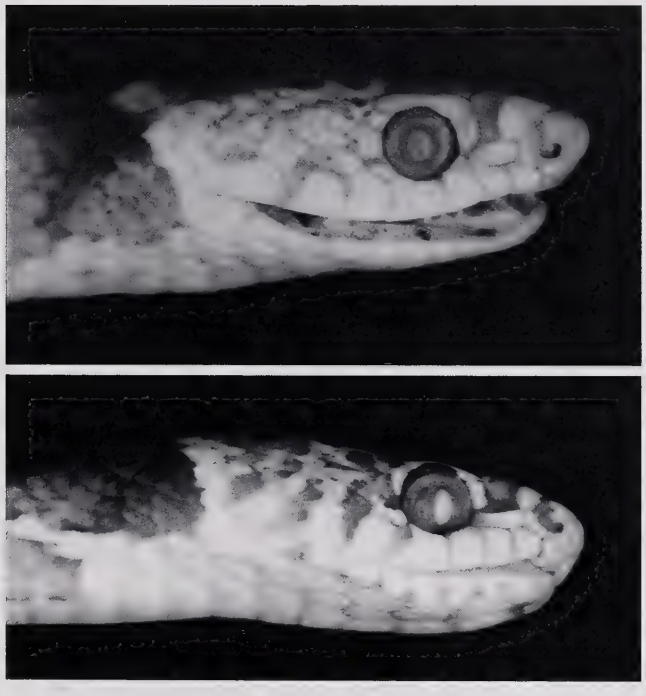


Figure 31. *Sibynomorphus vagrans.* Lateral views of heads. MCZ 17436 (top), MCZ 17442 (bottom). The ventrolateral portion of the dark prefrontal band is visible immediately in front of the preocular and extending to the upper edge of the loreal (see Fig. 30, left upper and lower).

However, the similarity between the two species ends there if my supposition that the name of *S. vagus* refers to its color pattern (see *Description* in its species account), because the color pattern of *S. vagrans* bears little resemblance to that of *S. vagus*.

Hemipenis

Inverted Hemipenis. The following description of the hemipenis of *Sibynomorphus vagrans* is based on the inverted organ of MCZ 17438, an adult male, 381 mm SVL. The organ extends to the suture between subcaudals 6 and 7. It is slightly bilobed, dividing at the level of the proximal edge of subcaudal 6. Total length of organ 12.5 mm, bilobed distally for approximately 1 mm. The major retractor muscle is divided proximally for 1–1.5 mm.

The hemipenis is capitate, and the capitulum bears well-developed papillate calyces. The sulcus spermaticus is on the

dorsal surface of the inverted organ and divides just within the capitulum; its tips end just short of the distal tip of the organ. The undivided portion of sulcus spermaticus is 5–5.5 mm in length; the divided portion is 6–6.5 mm in length. Proximal to the capitulum is a broad battery of robust spines encircling the entire organ; the battery is about three spines in width adjacent to the sulcus, broadening to about four or five spines in width on the asulcate side. The battery is separated from the capitulum by a narrow gap on the asulcate side, whereas the battery approaches the capitulum adjacent to the sulcus spermaticus. Proximal to the battery of enlarged spines, the hemipenis is ornamented with minute spinules, including the borders and lobes adjacent to a basal nude pocket.

The basal nude pocket is 4 mm long and extends from the base of the organ to the battery of spines. The pocket is located in the dorsomedial wall of the inverted organ and thus is probably somewhat lateral in the everted organ. On its asulcate edge, the pocket is bordered by a prominent lobe on its proximal half and a somewhat smaller lobe on the sulcate edge.

Everted Hemipenis. The left hemipenis of MCZ 17439 (adult male, 387 mm SVL) was everted from a preserved specimen according to techniques described by Myers and Cadle (2003) (Fig. 32). Before eversion, the hemipenis extended to the distal half of subcaudal 8. It was slightly bilobed, dividing at the suture line between subcaudals 7 and 8. Total length of the uneverted organ was 15.5 mm, divided for approximately 1 mm. The retractor muscle was divided for about 1 mm, each tip inserting onto a lobe of the hemipenis. After eversion, the hemipenis measured 16 mm total length. The divided portion of the sulcus spermaticus was 7.5 mm in length.

The everted hemipenis is nonbilobed or only very slightly bilobed, fully capitate, and with the sulcus spermaticus dividing within the capitulum. The lobes appear asymmetrical in the preparation (Fig. 32),

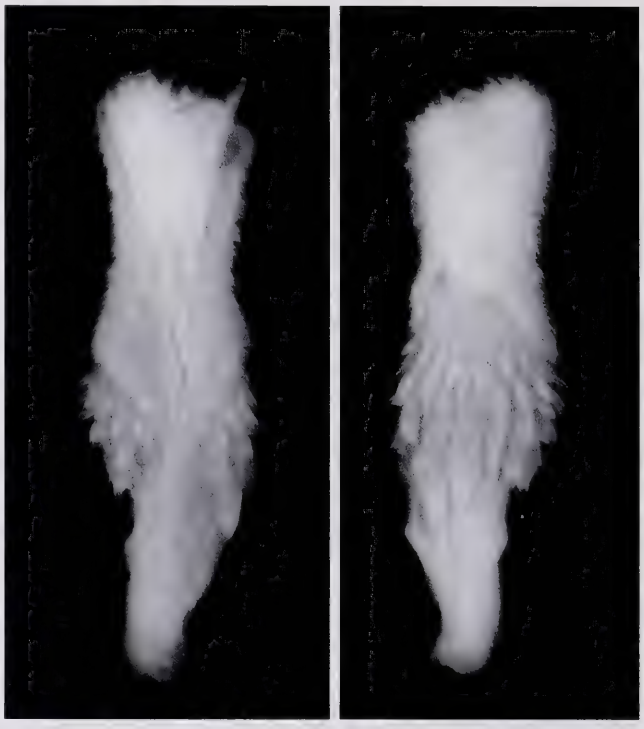


Figure 32. Hemipenis of *Sibynomorphus vagrans* in sulcate (left) and asulcate (right) views (MCZ 17439). This hemipenis was manually everted with the use of methods detailed by Myers and Cadle (2003).

but this very likely reflects a puncture in one of the lobes and its consequent lack of full inflation. The capitulum is ornamented with well-developed calyces surmounted by spinulate papillae. Proximal spinules are longer and apparently more mineralized than distal ones. A fringe of spinules borders the proximal overhang of the capitulum.

The sulcus spermaticus is more or less centrolineal but the tip of each branch passes somewhat laterally to lie nearly on the lateral sides of the lobes. The tips of the branches end on the outer periphery of the lobes, short of the center of the apex of the organ. Proximally, the hemipenis is ornamented with minute spinules. The midsection of the hemipenial body is ornamented with a battery of large, relatively straight spines encircling the organ; this battery is about three spines across adjacent to the undivided portion of the sulcus spermaticus and about four spines across on the asulcate side. Individual spines are relatively long, narrow, straight, and

hooked only at their tips (in contrast to the robust, strongly hooked spines typical of many colubrid hemipenes, including other *Sibynomorphus*). Proximal to the battery of spines on the asulcate side, but not clearly separated from the battery, are two large, hooked spines that are larger than those in the battery. A similar large spine is present near the undivided portion of the sulcus spermaticus.

A large nude pocket (total length 4 mm) is present basally on the lateral surface of the hemipenis; its distal end is bordered by the large hooked spines just mentioned. The pocket is also bordered on each side by a well-developed lobe, the asulcate lobe somewhat larger than the sulcate lobe. The entire basal portion of the organ below the encircling battery of spines (including the lobes on either side of the nude pocket, but not the pocket itself) is ornamented with minute spinules.

Distribution and Natural History

Sibynomorphus vagrans is known only from the type locality, Bellavista, Cajamarca Department, Peru, which lies at 421 m elevation in the subhumid inter-Andean valley of the Río Marañón (Amazonian versant) (Fig. 25). Dixon and Huey (1970: 38) described the general environment around Bellavista as "thorn scrub . . . [with] standing dead *Cereus* [columnar cactus]", although Dixon (personal communication, March 2007) stated that the area was wet enough to support coffee plantations; Dixon did not obtain *S. vagrans* at Bellavista 21–28 November 1968. Noble (1921) included a photographic appendix which shows "The [Río] Marañón at Bellavista"; his caption states that "the valley of the Marañón above Tutumberos [Amazonas Department on the Río Marañón a few kilometers downstream from Bellavista] is decidedly barren except for the cane and the dense thickets that crowd the river banks" (Noble, 1921: 493). All known specimens of *S. vagrans* were obtained by G. K. Noble, who collected around Bellavista in September 1916. Two specimens (MCZ 17451–52; SVLs 163 and 147 mm, respectively) have obvious umbilical scars and probably represent young of the year.

Sibynomorphus vagrans comes from a region frequently traveled by field biologists in northern Peru (e.g., Dixon and Huey, 1970; Dixon and Wright, 1975) because it lies along the main route from the coast to the upper Río Marañón, the stepping stone to the northern Peruvian Amazon. That the species is known only from specimens collected at the type locality nearly a century ago suggests that it might have a very localized distribution. Supporting this suggestion is that Noble did not obtain *S. vagrans* at another locality close to Bellavista—Perico—only about 35 km from Bellavista on the same side of the Río Marañón. The MCZ catalogues record more than 750 reptiles obtained by Noble at Bellavista and more than 300 at Perico.

According to his field notes and Noble (1921), Noble used local resident collectors ("frog hounds") to obtain specimens on the 1916 expedition to Peru. He obtained 27 specimens of *Sibynomorphus vagrans* at Bellavista (it was the most abundant snake in the collection), which suggests that the species was relatively common at that time. These specimens account for more than twice as many as the next most abundant snake represented in the Bellavista collection (12 specimens of *Leptodeira septentrionalis*; see Duellman, 1958: 80), and 41% of the total number of snakes from that locality (66 specimens representing seven species of snakes according to the online catalogue of the MCZ collection).

An Enigmatic Specimen from "Bellavista" Referred to *Sibynomorphus oneilli*

Apart from the type series, MUSM 2258 (Fig. 33) is the only specimen known to me that has been referred to *Sibynomorphus vagrans* (as reflected in the MUSM catalogues). According to the MUSM catalogues, MUSM 2258 was taken from the stomach of a "*Micrurus mertensi*" (MUSM

Figure 33. *Sibynomorphus* cf. *oneilli* from "Bellavista" (Peru) of unknown location (MUSM 2258). Male, 328 mm SVL.

2256) collected 25 July 1958 from "Bellavista"; the catalogue entry for the department "Cajamarca" might have been added at a later time. The specimen is problematic because many of its characteristics are unlike specimens of *S. vagrans* of the type series (Table 1) and, in fact, are more like *S. oneilli.* However, no species of *Micrurus* is recorded from the range and elevations known for *S. oneilli,* as judged from distribution maps and elevational data in Campbell and Lamar (2004). Only two known localities for *S. oneilli,* the type locality at 1,646 m and Hacienda Santa Rosa at 1,800 m, are at elevations that seem likely at all to harbor *Micrurus* species, although it is certainly possible that *S. oneilli* occurs at lower elevations as well. Resolving the identity of the *Sibynomorphus* should go hand in hand with study of the *Micrurus* and the locality. I have been unable to undertake a thorough study of MUSM 2256 in comparison with other Peruvian *Micrurus,* and, like the *Sibynomorphus,* it has some unusual characteristics. I herewith present my assessment of these specimens but leave the ultimate resolution of this problem to others.

The locality for the two specimens, "Bellavista," could refer to the well-known herpetological locality in the Río Marañón valley of Cajamarca Department, the type locality of *Sibynomorphus vagrans.* However, a search of the GeoNet Names Server for "Bellavista" in Peru recovered 70 entries, of which several were within the conceivable ranges and elevations of *S. vagrans* and *S. oneilli.* Moreover, the identity of MUSM 2256 as "*Micrurus mertensi*" seems questionable if the locality is the "Bellavista" of the type locality of *Sibynomorphus vagrans. Micrurus mertensi* is a snake of the Pacific coastal region of northern Peru (Campbell and Lamar, 2004), whereas the very similar species, *M. peruvianus,* is found in the upper Río Marañón valley and, indeed, is known from the "Bellavista" of Noble's collections (specimens in MCZ). Nonetheless, MUSM 2256 has some characteristics that are more similar to *M. mertensi* than *M. peruvianus,* and the relationship (or conspecificity) of these two very similar species is unclear (Campbell and Lamar, 2004).

MUSM 2256 is a male tricolored coral snake (without triads), 655 mm total length, 567 mm SVL, 225 ventrals, 46 subcaudals, 1 + 1 temporals, 7 supralabials (3–4 touching the eye), 7 infralabials, 1 preocular, and 2 postoculars. The size is more than 100 mm longer than the maximum reported for *M. peruvianus* but is typical for *M. mertensi.* The ventral count is 23 more than the maximum for male *M. peruvianus* and 4 more than the maximum

reported for male *M. mertensi* (data from Campbell and Lamar, 2004). Without further comparative study of *Micrurus* from northern Peru, I do not feel confident in making a call on the identity of MUSM 2256.

The *Sibynomorphus,* MUSM 2258 (Fig. 33), is a male, 425 mm total length, 107 mm tail length (25% of total), with 15–15–15 dorsal rows, 157 ventrals (+2 preventrals), 72 subcaudals, anal single, 8 (4–5)/7 (3–4) supralabials, 11/10 infralabials (the first pair in contact behind the mental), a small preocular on each side superior to loreal, loreal and preocular in contact with eye, 2/2 postoculars, 2/2 primary temporals, 2/3 secondary temporals, and 2 pairs of chin shields.

MUSM 2258 is distinctly banded the whole length of the body with 39 black crossbands (Fig. 33). The anterior crossbands are broader than the posterior ones; a series of crossbands at midbody is interrupted middorsally and tend to alternate. The first (neck) band is 4 scales wide; then follow two bands that are 3 scales wide, whereas most of the crossbands on the body are 1–1.5 scales wide. Interspaces are 1–2 scales wide anteriorly; most of the interspaces are 3 scales wide, occasionally 4. The top of the head is gray with an irregular smudged spot on each parietal; the remainder of head is immaculate grayish. The gular region is grayish and unmarked. The venter is heavily checkerboarded with black squarish and trapezoidal markings on a grayish white ground color (Fig. 33).

MUSM 2258 differs from the type series of *Sibynomorphus vagrans* in several scale and pattern characteristics. Compared with male *S. vagrans,* MUSM 2258 has 2 more ventrals and 8 fewer subcaudals than the next closest respective counts among male specimens of *S. vagrans* (Table 1). The supralabial pattern on one side, 7 (3–4 touching the eye), was observed in no other specimen of *S. vagrans,* although these patterns are highly variable within species. Perhaps the most striking differences between MUSM 2258 and specimens of *S. vagrans* are notable differences in the dorsal and ventral patterns. For these comparisons, the contrasting characters of *S. vagrans* are indicated in parentheses: in MUSM 2258 the body is distinctly crossbanded for its entire length (distinctly banded only anteriorly; compare Figs. 28, 29, 33); the anterior broad crossbands are 3–4 scales wide (generally 5 or more but occasionally 3 or 4); the top of the head is mostly uniform grayish (top of the head ornately patterned with dark irregular markings; Fig. 30); the venter is densely patterned with bold black markings on a pale ground color (venter immaculate or with scattered obscure dark spots). The band across the prefrontal scales typical of *S. vagrans* (see above description) is indistinct in MUSM 2258 and could only be discerned with close inspection; it would certainly not have been noticed had I not been looking carefully for it, whereas in typical *S. vagrans,* this band is very obvious (as noted also by Peters, 1960: 162). MUSM 2258 also lacks the pale angular nape collar characteristic of *S. vagrans*; although MUSM 2258 has a pale nape collar, it is more rounded than is characteristic of *S. vagrans* and is separated middorsally from the parietal scales only by slightly more than 1 nuchal scale, compared with about 3 scales in *S. vagrans.*

On the other hand, all of the scutellation characteristics of MUSM 2258 are typical of *Sibynomorphus oneilli* (Table 1), including ventral and subcaudal counts that are at the approximate midrange of the corresponding counts of male *S. oneilli.* Moreover, the color pattern of MUSM 2258, including details of the dorsal crossbands, the heavily patterned venter, the uncomplicated pattern atop the head, and details of the pale nape collar, are much more similar to other specimens of *S. oneilli* (see above species account) than to *S. vagrans.* In conclusion, were it not for uncertainties concerning the locality and its association with a *Micrurus* of uncertain identity, I would unhesitatingly refer

Figure 34. *Sibynomorphus vagus.* Illustration of the holotype from Jan and Sordelli (1860–1881: 37[e] Livraison, pl. VI, fig. 2).

MUSM 2258 to *Sibynomorphus oneilli* rather than to *S. vagrans.* Further research on the identity of the *Micrurus* and possible identities of the "Bellavista" where the specimens were collected is needed to confidently resolve the present ambiguities.

Sibynomorphus vagus (Jan) Figures 34–39

Leptognathus vagus Jan, 1863: 100–101. Holotype (Fig. 34), a specimen in the Museo Civico di Storia Naturale, Milan (not examined; probably destroyed during the bombing of 1943), Jan and Sordelli, 1860–1881: 37[e] Livraison, pl. VI, fig. 2. Type locality: "Hong Kong." Cope (1868: 136) examined the holotype and stated that it is "probably South American."

Leptognathus vaga: Cope, 1868: 136. [brief description of the holotype; see below]

Pareas vagus: Boettger, 1888: 145.

Pseudopareas vagus: Boulenger, 1896: 462. Werner, 1922: 200. Dunn, 1923: 187.

Pseudopareas vagus vagus: Amaral, "1929"a [1930]: 33; "1929"b [1930]: 201; "1929"c [1930]: 75.

Sibynomorphus vagus: Peters, 1960: 164, 1965: 14. Rossman and Thomas, 1979. Rossman and Kiziriian, 1993. Orcés and Almendáriz, 1989. Scrocchi et al., 1993. Carrillo de Espinoza and Icochea, 1995.

Notes on the Holotype of *Sibynomorphus vagus*

The holotype of *Sibynomorphus vagus,* illustrated by Jan and Sordelli (1860–1881) (Fig. 34), was a specimen in Milan's Museo Civico di Storia Naturale. Jan's (1863: 100–101) diagnosis of *Leptognathus vagus* appeared in a key to the genus, in which *L. vagus* was diagnosed by the following characteristics: [15] scale rows, loreal in contact with the eye, and 8 supralabials. Jan and Sordelli's (1860–1881) illustration of the holotype shows the following characteristics: body slightly compressed; smooth dorsal scales in 15 rows anteriorly and at midbody; supralabials 8 with 4–5 touching the eye on each side, 2–4 bordering the loreal; infralabials 10/10, the first pair in contact behind the mental; three pairs of polygonal chin shields (the first pair somewhat elongate) followed by three preventrals (the first with a partial suture); loreal and preocular bordering the anterior edge of the eye (preocular superior to loreal); loreal longer than tall; postoculars 2/2; primary temporals 1/1, secondary temporals 2/2, tertiary temporals 2/2 (with the upper secondary temporal fused with the upper tertiary temporal on the left side); anal single; subcaudals 50. The anterior body has a series of irregular lateral vertical markings one scale row or less in width and separated by 2–3 rows. Middorsally is a series of smaller irregular

flecks that are aligned with or slightly offset from the lateral series. Top of the head without distinct pattern (stippled uniformly); a slight concentration of dark pigment is on suture lines of the posterior supralabials. The ventrals and subcaudals are heavily patterned with bold half-moon markings; on the posterior body, these tend to align into longitudinal rows on the outer portion of the ventrals.

The characters of the holotype as derived from Jan and Sordelli's illustration are consistent with the variation within the sample of *Sibynomorphus vagus* I examined (Table 1) except for the low number of subcaudals. On this basis, Dunn (1923) inferred that the holotype must be a female, which seems a reasonable assumption. Cope's (1868: 136) brief description of the holotype contains two remarks at variance with the illustration by Jan and Sordelli. Cope stated that "of the preoculars nothing can be said" (the illustration shows the preocular and loreal contacting the eye) and "four pairs of genials" (the illustration shows three pairs of genials, but the first preventral has a partial suture and may have been the fourth pair of genials recognized by Cope).

Cope (1868) first suggested that the holotype of *Sibynomorphus vagus* came from South America, but no other specimens were reported until Dunn (1923) described the series obtained by G. K. Noble at Huancabamba, Peru (Piura Department), in 1916. Dunn (1923: 187) merely stated that Noble's specimens "apparently represent the type of the genus [*Pseudopareas*]." Only half a dozen specimens of *S. vagus*, all from the vicinity of Huancabamba, have been obtained since Noble collected his specimens (see *Specimens Examined and Locality Records*).

Dunn (1923) undoubtedly associated Noble's series with the illustration by Jan and Sordelli because of the close match to details of scutellation and pattern. However, those details also largely match specimens of the later-described *S. oneilli* with fragmented dorsal crossbands, as described herein (see species account and Table 1). The subcaudal count in Jan and Sordelli's illustration (Fig. 34) is equally low for both *S. oneilli* and *S. vagus*. Only the details of the temporal scale patterns in the holotype of *S. vagus* (1 + 2 + 2) more closely match specimens from Huancabamba than they do specimens of *S. oneilli*, as indicated in the discussion of nonbanded specimens of *S. oneilli* from the Río Santa valley and comparisons of them to *S. vagus* (see Tables 1 and 3 and the species account for *S. oneilli*). Thus, even though the differences in temporal scales between these two species are not absolute, the preponderance of characters discernible in the illustration by Jan and Sordelli (1860–1881) matches *S. vagus* sensu Dunn (1923) more closely than *S. oneilli*. Confirmation of the ventral count and sex of the holotype would provide corroboration (see Table 1), but that might be impossible if the specimen was destroyed during the bombing of 1943, as was the case with most or all of the older specimens in the Museo Civico di Storia Naturale.

Diagnosis

Sibynomorphus vagus is characterized by a relatively low number of ventrals (144–152 in males, 151–158 in females) and subcaudals (60–65 in males, 56–60 in females), a dorsal pattern lacking well-defined crossbands or with narrow irregular crossbands (much narrower than interspaces anteriorly), and a venter heavily marked with large squarish spots, often concentrated laterally on the ventral plates (Figs. 34, 35). The top of the head is relatively unmarked or has an obscure pattern. Dorsal crossbands, when present, are usually not well defined, are often present only anteriorly, and usually have irregular borders.

Sibynomorphus vagus differs from other species of the genus in northern South America except *S. vagrans* and *S. oligozonatus* in having a low number of ventral scales. *Sibynomorphus vagrans* is similar

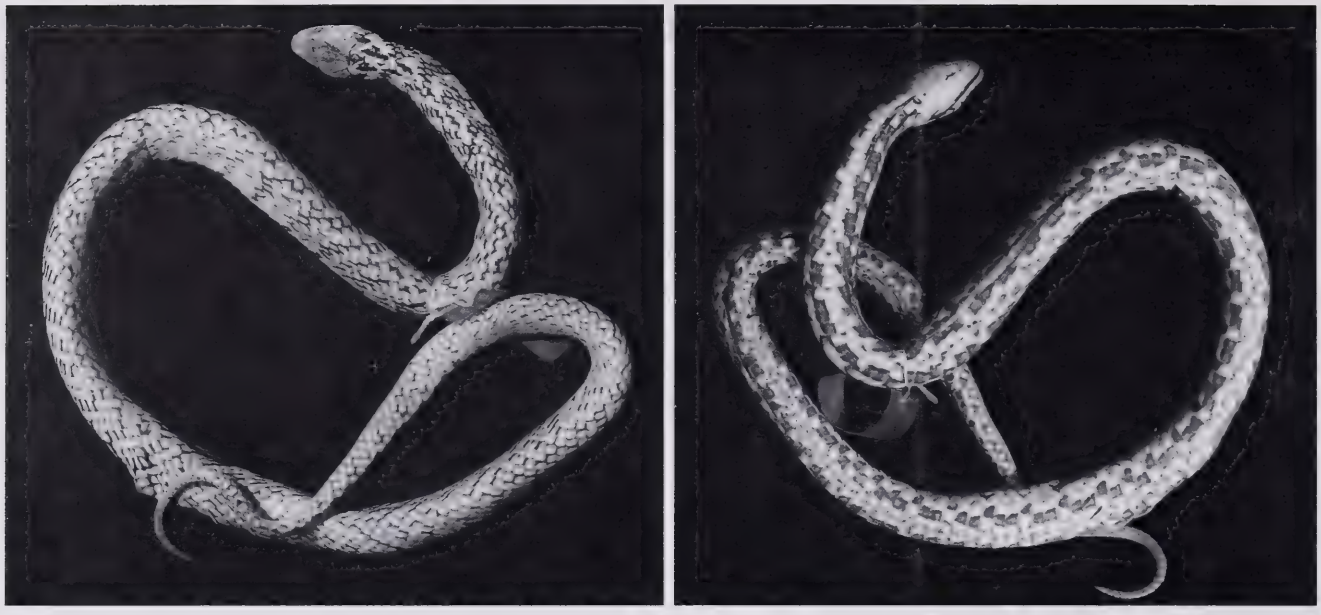


Figure 35. *Sibynomorphus vagus* from Huancabamba, Cajamarca Department, Peru (MCZ 17422). Male, 291 mm SVL.

to *S. vagus* in ventral counts (Table 1) but has bold, well-defined anterior crossbands that are much broader than the interspaces (Figs. 28, 29), has more subcaudals (80–87 in males, 72–79 in females), and has a longer tail than *S. vagus* (Table 1). *Sibynomorphus oligozonatus* differs from *S. vagus* in having well-defined bold anterior crossbands that are much broader than the interspaces (Figs. 1, 2, 4, 5) and a relatively unpatterned venter (heavily marked in *S. vagus*), and in lacking a preocular scale (present in *S. vagus*). *Sibynomorphus petersi* and *S. williamsi* have >160 and >170 ventrals, respectively (sexes combined), and different color patterns. Male and female *S. oneilli* have 152–168 and 163–173 ventrals, respectively.

Description

Size and Scutellation. Descriptive data for *Sibynomorphus vagus* are presented in Table 1. The largest specimen is a male, 483 mm total length, 368 mm SVL; the largest female is 408 mm total length, 326 mm SVL. Tail 23–24% of total length in males, 20–21% of total length in females. Body only slightly compressed. Dorsal scales in 15–15–15 rows, smooth. The vertebral row is very slightly broader to about 1.5 times as broad as the paravertebral rows. Ventrals 144–152 (averaging 149) in males, 151–158 (averaging 154) in females. Anal single. Subcaudals 60–65 (averaging 63) in males, 56–60 (averaging 57) in females. Loreal and preocular bordering eye (preocular superior to the loreal). Loreal longer than tall. Postoculars 2 (rarely 1). Primary temporals usually 1 (rarely 2). Secondary temporals 2 (rarely 3). Tertiary temporals usually 2 (range 0–3). Supralabials 7 or 8, usually with 4–5 bordering the eye (occasionally 3–4). Infralabials usually 9 or 10 (range 8–11). One pair of infralabials in contact behind the mental (8 specimens), or a single infralabial contacts two on the opposite side (2 specimens). Chin shields in 2 pairs ($N = 1$), 3 pairs ($N = 7$), or 4 pairs ($N = 2$). Maxillary teeth 14–16 ($N = 5$). The pupil is prolate (Myers, 1984) in preserved specimens.

Sexual Dimorphism. The largest specimen is a male (Table 1), but with only two adult females and three adult males, it seems likely that this is a sampling artifact rather than an uncommon pattern of sexual dimorphism (none of the other species of *Sibynomorphus* show this unusual pattern, although *S. petersi* comes close). Other sexually dimorphic characters in *Si-*

bynomorphus vagus follow the typical colubrid patterns. Compared with females, male *S. vagus* have significantly fewer ventrals ($t = 2.680$, df = 8, $p < 0.05$), significantly more subcaudals ($t = 7.200$, df = 6, $p < 0.001$), and greater relative tail lengths (Table 1). Dunn (1923: 187) commented that females have less ventral spotting than males, but that difference is not apparent considering the new material (see also Rossman and Kizirian, 1993, fig. 2).

Color in Life. Unknown. Cope (1868: 136) might have seen the relatively freshly preserved holotype, which he described as "above wood-brown, with indistinct cross series of spots. Below yellowish, tessellated with brown."

Color in Preservative. The dorsal ground color is gray to grayish brown. Anteriorly, there may be a series of ill-defined, irregular, narrow (one scale row in width) crossbands; poorly defined reticulations; or a vague dark network (Figs. 35, 36). Posteriorly, the dorsum can be unicolor grayish, with a poorly defined obscure network, or poorly defined crossbands can extend for a variable length along the body (see Rossman and Kizirian, 1993: fig. 2). The venter is usually boldly marked with dark squarish or half-moon–shaped markings or spots on a gray to grayish brown ground color; in some specimens (e.g., MCZ 17420), these markings are reduced to small dark spots mainly concentrated on the anterior venter. The top of the head is gray to grayish brown, usually with a few scattered darker spots, especially on the posterior head plates. The lateral surface of head is generally unmarked and lacks extensively darkened suture lines on the labial scales (Figs. 37, 38).

There seemingly is no substantive ontogenetic change in color pattern, as several small individuals, including one with a visible umbilical scar (MCZ 17426; 137 mm SVL), do not consistently differ from larger ones in pattern.

Etymology. The common meaning of the specific epithet, *vagus,* is wandering or roaming. However, the word can also mean diffuse or indefinite (as in vague). I suspect this is a reference to the diffuse dorsal pattern of *Sibynomorphus vagus* compared with other species of *Leptognathus* known at the time of its description—as seen especially by comparing the illustration of *S. vagus* with the other species illustrated on the same plate by Jan and Sordelli (1860–1881): *Dipsas incerta, S. mikanii,* and the Asian colubrid *Pareas laevis* (all in the genus *Leptognathus* at the

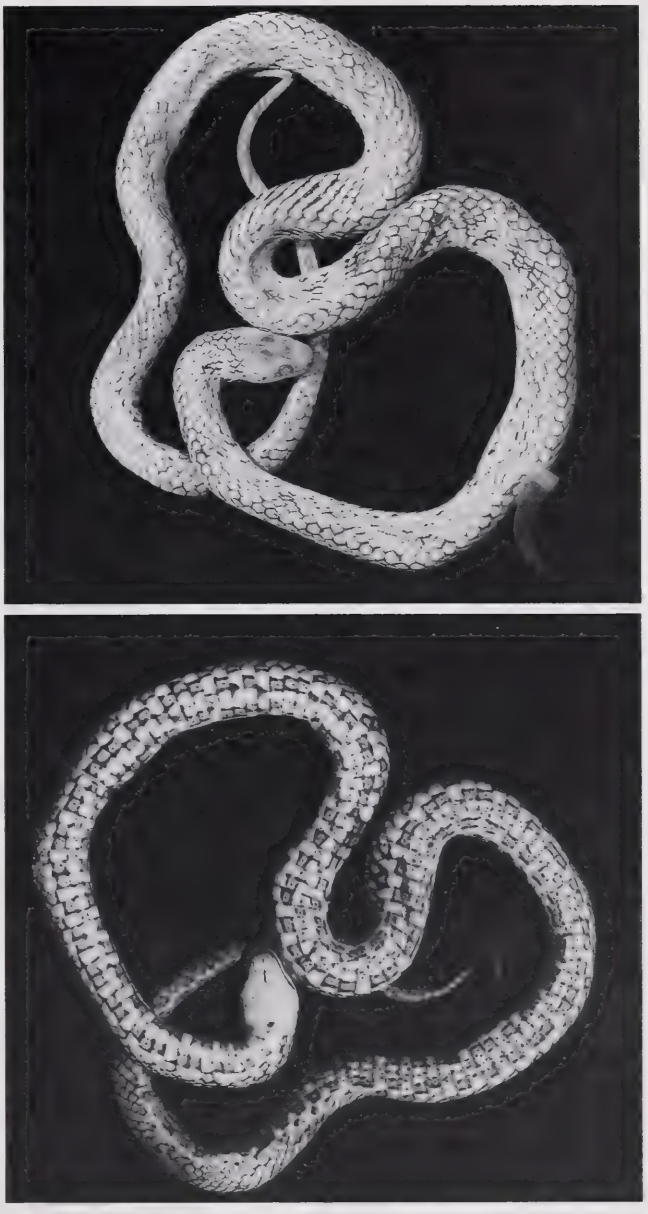


Figure 36. *Sibynomorphus vagus* from Huancabamba, Cajamarca Department, Peru (MCZ 17421). Male, 368 mm SVL.

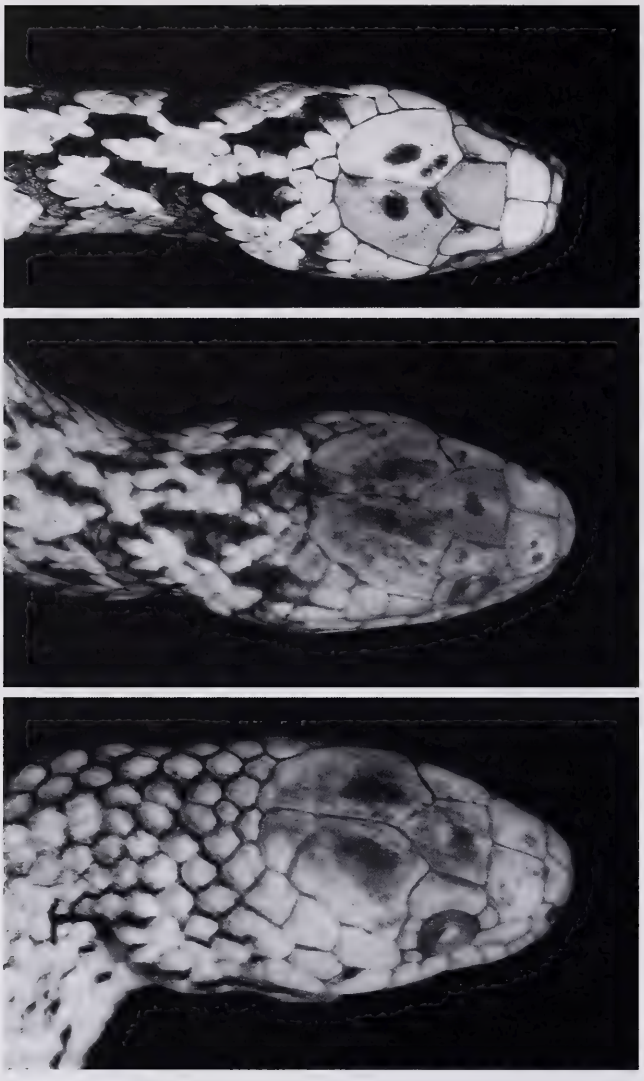


Figure 37. *Sibynomorphus vagus.* Dorsal views of heads. Top to bottom: KU 219121, MCZ 17422, MCZ 17421. The dark spots or smudges on the parietal scales are characteristic of most specimens of *S. vagus.*

Figure 38. *Sibynomorphus vagus.* Lateral views of heads. KU 219121 (top), MCZ 17422 (bottom).

time); these are much more boldly marked than *S. vagus.*

Hemipenis

Inverted Hemipenis. The following description of the inverted organ of *Sibynomorphus vagus* is based on MCZ 17422 (adult male, 291 mm SVL). The hemipenis extends to the level of the suture between subcaudals 10 and 11. It is slightly bilobed, dividing at the level of the suture between subcaudals 9 and 10. Total length of the organ 15 mm, divided distally for 2 mm. The major retractor muscle is divided for approximately 1–1.5 mm at its insertion.

The organ is ornamented with minute spines basally and distally is fully capitate. The capitulum is ornamented with papillate calyces. The sulcus spermaticus (in the dorsal wall of the organ) divides within the capitulum at the level of the distal portion of subcaudal 4; its branches end at the distal tips of the lobes. The undivided portion of the sulcus spermaticus is 6 mm long; its divided portion is 7.5 mm long.

Proximal to the capitulum, a battery of spines completely encircles the hemipenial body. The battery is three spines in width adjacent to the sulcus spermaticus and broadens to four or five spines wide on the asulcate side. A very long basal nude pocket, 4.5 mm in length, extends in the dorsomedial wall of the organ (lateral surface in the everted condition) from the base of the hemipenis to the battery of spines. The distal end of the pocket is nested within the battery of spines. The asulcate edge of the pocket is bordered by a prominent lobe extending from the base to the midpoint of the pocket. The lobe is a narrow flange of tissue proximally, and is most prominent at about the midpoint of the

Figure 39. Hemipenis of *Sibynomorphus vagus* in sulcate view (MCZ 17421). This hemipenis was manually everted with methods detailed by Myers and Cadle (2003).

pocket. The hemipenis proximal to the encircling battery of spines is ornamented with minute spines everywhere except within the nude pocket.

Everted Hemipenis. The left hemipenis of MCZ 17421 (adult male, 368 mm SVL) was everted from the preserved specimen with the use of techniques described by Myers and Cadle (2003) (Fig. 39).

Before eversion, the hemipenis extended to the suture between subcaudals 9 and 10. It was slightly bilobed, dividing at the suture between subcaudals 7 and 8. Total length of the organ was 15.5 mm, divided for approximately 2 mm. The retractor muscle was divided for approximately 1.5 mm, each tip inserting onto a lobe of the hemipenis. At the distal end of the inverted hemipenis, a fold of the tissue that would form the apex of the everted organ extends between the inverted lobes. Consequently, the distal end of the inverted organ was rather trilobed, with a fold of the capitular tissue extending posteriorly between the branches of the divided retractor muscle, and larger than either lateral lobe (i.e., tissue that would become the lobes of the everted organ). The folding of the apical tissue is perhaps only a convenient way of accommodating tissue that is incorporated into the expanding apical region of the everted organ; it has no apparent counterpart in the everted organ. This peculiar structure was not noted in the above-described inverted hemipenis (MCZ 17422).

The everted organ was 15 mm in length and the sulcus spermaticus was divided for 7 mm. The hemipenis is fully capitate, with only a very slight indication of bilobation (perhaps nonbilobed if fully expanded and inflated, which was not attempted because of the delicacy of the preparation). The sulcus spermaticus divides within the capitulum and its tips are more or less centrolineal in orientation, but they pass somewhat laterally and end at the lateral edges of the apex of the organ. The capitulum is ornamented with well-developed papillate calyces. Proximal to the capitulum is a battery of large hooked spines encircling the organ, three to four spines across all around. A large basal nude pocket (3.5 mm in length) is on the lateral side of the organ. It is bordered on its asulcate side by a large lobe and toward its distal end by a pair of large spines, one on each edge. These spines are larger than any in the battery encircling the organ. The base of the hemipenis below the battery of spines, including the lobes bordering the nude pocket (but not the tissue within the pocket) is ornamented with minute spines.

The hemipenes of *Sibynomorphus vagus* and *S. vagrans* are very similar to one another but differ in the shape of their enlarged spines. The spines on the organ of *S. vagus* are comparatively shorter and more robust, and the entire spine forms a curved hook, whereas the enlarged spines on the hemipenis of *S. vagrans* are rather narrow, somewhat straight, and hooked only at their distal tip.

Distribution and Natural History

Sibynomorphus vagus is known only from the vicinity of Huancabamba, Piura

Department, Peru (Fig. 25). The documented elevational range is 1,810 to 1,920 m. Huancabamba lies in the steep valley of the Río Huancabamba, a tributary of the Río Marañón and thus is on the Amazonian versant (and not the Pacific slopes as occasionally stated; e.g., Rossman and Thomas, 1979: 6).

Noble (1921) described the general environment surrounding Huancabamba during August 1916 (when the series in the MCZ was collected) as follows:

> Huancabamba lies on a slope overlooking a mountain torrent. The country on either side is steep and barren. Still, there are pockets of less dry areas and in these we found tropical animals and plants. Huancabamba seemed to be the mingling point of several diverse biotas. Bananas and cacti grew side by side . . . the dominant facies of the fauna seemed tropical, although much out of place in such a barren region.

Parker et al. (1985: 171) described the area in June/July 1980:

> Huancabamba lies in a narrow rain-shadow valley. . . . Although this arid valley is densely settled and intensely cultivated, a few small remnants of desert scrub remain within walking distance of the city. The vegetation [of this desert scrub] is composed of dense shrubbery and scattered *Acacia* trees and clumps of columnar cacti. The farmlands above this dry terrain eventually give way to humid forest at about 2150 m.

Noble's field notes (AMNH Herpetology Department archives) indicate that he worked in and around Huancabamba from 7 to 27 August 1916. There are references in his notes during this period to collecting birds (most references), small mammals, and frogs (including *Gastrotheca*), but no mention of snakes. His entry for 27 August includes the comment "There are so few birds or beasts of interest about Huancabamba that I have decided to move on to some place else."[14]

Some literature records for "*Sibynomorphus vagus*" are questionable or erroneous. Lehr et al. (2002: 134) referred two specimens from the Pacific slopes of southern Ancash Department, Peru (SMF 80048, MUSM 20583) to *S. vagus*; these specimens are *S. petersi* (see above species account). Specimens from Ancash, Cajamarca, La Libertad, and San Martín Departments were also identified as *S. vagus* (Carrillo de Espinoza and Icochea, 1995). These records were presumably based on the specimens I refer to *S. oneilli* (see species account in *New Material of* Sibynomorphus oneilli *from Ancash and Libertad Departments, Peru*), but I did not see specimens from San Martín.[15]

Very little is known of the natural history of *Sibynomorphus vagus*. Six specimens were taken from under rocks in a semiurban setting ("outside a tourist hotel") or in a cleared field in January 1991 (Rossman and Kizirian, 1993). KU 135180 was collected 10 May 1970, and the MCZ series was collected in August 1916. The smallest specimen examined, MCZ 17426 (SVL 137 mm), has the umbilical scar beginning to fuse.

Sibynomorphus williamsi Carrillo de Espinoza Figures 40–42

Sibynomorphus williamsi Carrillo de Espinoza, 1974: 3. Holotype, MUSM 2170 (original number "Of. 0492" given in the original description)[16] (Fig. 40). Type locality: "Jicamarca. Radio-observatorio. Dis-

[14] The AMNH Herpetology Archives contain only Noble's notes for July–August of the 1916 Harvard Peruvian Expedition, with coverage to just past Huancabamba. The whereabouts of the remainder of the notes (through September, covering the important Noble localities Bellavista and Perico) is unknown. A possible repository is the archives of Harvard University, but their existence was not pursued during this study. The portion of the notes at AMNH contain almost no information on the collections, essentially being a diary of the journey rather than actual field notes.

[15] If the specimen(s) from San Martín are found and also prove to be *Sibynomorphus oneilli*, it would be only the second record, in addition to the holotype, from east of the Río Marañón.

[16] The herpetological collections of the MUSM originally used separate numbering systems for different taxonomic groups; hence "Of.," referring to "Ofidios." With reorganization of the collection commencing in the 1980s, all specimens were renumbered in a continuous series.

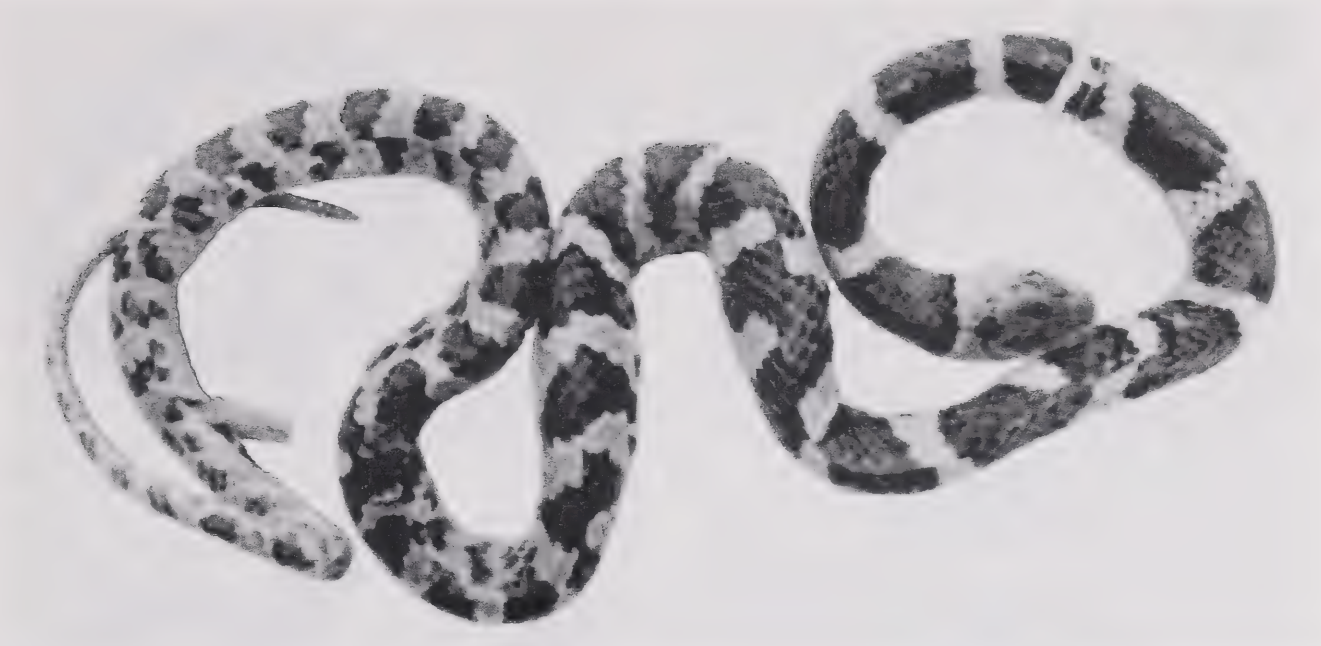


Figure 40. *Sibynomorphus williamsi.* Holotype (MUSM 2170) from Jicamarca (vicinity of Lima). Male, 404 mm SVL.

trito Lurigancho, Provincia Lima, Departamento Lima" [Peru].

Sibynomorphus williamsi has heretofore been reported only from coastal "lomas" formations in the Department of Lima (Carrillo de Espinoza, 1974); see *Distribution and Natural History* below. Specimens in the MUSM show that the species has a broader distribution in the central coastal region of Peru, including Andean foothills and slopes.

Notes on the Holotype of *Sibynomorphus williamsi*

The type series of *Sibynomorphus williamsi* consisted of a male holotype (MUSM 2170) and six female paratypes. I studied the holotype and four of the six paratypes. Three of the paratypes were from the type locality (MUSM 2173–74; the other not seen), one from the Lomas de Lurín (MUSM 2171), one from the Lomas de Pachacamac (not seen), and one from the Lomas de Lachay (MUSM 3400). These localities, except the Lomas de Lachay, are in the immediate vicinity of the city of Lima; the Lomas de Lachay are on the coast approximately 80–90 km NW of Lima (see Fig. 43).

The holotype of *Sibynomorphus williamsi* (MUSM 2170; Fig. 40) is an adult male in good condition, 530 mm in total length, 126 mm tail length (tail 24% of total length). It has 15–15–15 dorsals, 174 ventrals (+2 preventrals), single anal, 67 subcaudals, 0 preoculars (loreal and prefrontal border the anterior edge of the eye), 3/2 postoculars, 6/6 supralabials with 3–4 bordering the eye on each side (the third supralabial on the right side is divided horizontally to form a "subocular"), 10/11 infralabials, 3 + 4 + 4 temporals on each side, 3 pairs of polygonal chin shields, 1 pair of infralabials in contact behind the mental, and 13 maxillary teeth. It has 35 dorsal crossbands or blotches. The right hemipenis is everted.

I am unable to reconcile my data for the holotype with some scale counts and measurements given by Carrillo de Espinoza (1974: 4, table 1), who reported 186 ventrals, 63 subcaudals, and 10/10 infralabials in the holotype, and body measurements of 545 mm ("cuerpo"), 118 mm ("cola"), and 20 mm ("cabeza"). The high number of ventrals and low number of subcaudals (see *Description*) suggest that data for one of the female paratypes were mixed up

with those of the holotype, but data presented for the paratypes (Carrillo de Espinoza, 1974: table 1) do not closely match my data either. Nonetheless, our observations of the holotype are of the same specimen, as indicated by the sex and locality of the specimen and other details, such as the divided right third supralabial (shown in Carrillo de Espinoza, 1974: fig. 4), the everted right hemipenis, and details of banding pattern (Fig. 40; Carrillo de Espinoza, 1974: fig. 1).

Diagnosis

Sibynomorphus williamsi is characterized by a high number of ventral scales (173–182 in males, 181–188 in females), usually 6 supralabials with 3–4 bordering the eye, a relatively short tail (21–24% of total length in males, 19–22% in females), and a head distinctly wider than the neck, with the first dorsal crossband usually extending up onto the wide posterior part of the head. The dorsum is strongly crossbanded from head to tail (35–48 bands; posterior bands might be broken into dorsal and lateral blotches, offset to varying degrees, but they retain their boldness). Anterior crossbands can be twice the width of posterior crossbands, but they are always wider than the pale interspaces, which are 1–2 scale rows wide the length of the body.

Sibynomorphus williamsi differs from other species of the genus in western South America as follows (see also previous species accounts). *Sibynomorphus vagrans* and *S. vagus* have fewer ventral scales (≤160 in each case) and different color patterns. *Sibynomorphus oligozonatus* has a short, blunt snout; a head that is not distinctly wider than the neck; and fewer ventrals in males (145–163 in three specimens). In *S. williamsi,* the dorsal crossbands (including posterior blotches) are bold the entire length of the body (Figs. 40, 41), whereas in *S. oligozonatus,* the anterior crossbands are much more well defined than the posterior blotches. *Sibynomorphus petersi* and *S. oneilli* differ from *S. williamsi* in color patterns (see their species accounts) and in having 8 supralabials with 4–5 touching the eye.

Figure 41. *Sibynomorphus williamsi.* Representative specimens in dorsal view. Top: MUSM 3025 from Ancash Department (female, 427 mm SVL). Bottom: MUSM 3137 from Lima Department (male, 435 mm SVL).

Description

Size and Scutellation. A summary of character data for *Sibynomorphus williamsi* is presented in Table 1. The largest specimen is a female 718 mm total length, 561 mm SVL; largest male is 563 mm total length, 435 mm SVL. Tail 21–24% in males, 19–22% of total length in females. Body somewhat compressed; the head is distinctly wider than the neck. Dorsal scales in 15–15–15 rows. Vertebral row not, or only scarcely, enlarged. Ventrals 173–182 (averaging 177) in males, 181–188 (averaging 184) in females. One to three preventrals precedes the ventral

plates. Anal single. Subcaudals 67–73 (averaging 69) in males, 56–66 (averaging 62) in females. Loreal and prefrontal bordering anterior edge of eye (no separate preocular); loreal longer than tall. The first supralabial usually makes broad contact with the loreal (occasionally only narrow contact); supralabials 2 and 3 also border the loreal. Postoculars 2 (occasionally 3). Primary temporals 2 or 3, secondary temporals usually 3 or 4 (rarely 2), tertiary temporals usually 3 or 4 (rarely 5). Supralabials 6 with 3–4 touching the eye (rarely 7 with 3–4 touching the eye). Infralabials usually 10 (range 8–11). One pair (N = 17 specimens) or two pairs (N = 1) of infralabials in contact behind the mental. Chin shields in three pairs (N = 11) or two pairs (N = 3). Maxillary teeth 12–14 (N = 6).

The consistency of the fused preocular–prefrontal is remarkable in this species compared with some other Dipsadini (e.g., *Sibynomorphus oneilli, S. petersi, S. vagrans,* and various *Dipsas* spp.; Table 1; Cadle, 2005; Cadle and Myers, 2003). No separate preocular is present in any specimen. Three specimens have unusual configurations of the loreal and surrounding scales: in MUSM 19236, the loreal is expanded posteriorly so that the prefrontal contacts the eye very narrowly; MUSM 3137 and MUSM 2173 show the same condition on one side only; additionally, on the contralateral side of MUSM 2173, the loreal contacts the supraocular, occluding contact between the prefrontal and eye. A few other variations were observed: one specimen (MUSM 19236) has an irregular row of suboculars on the left side separating the supralabials from the eye, and a single subocular on the right side of the holotype is formed by horizontal division of the third supralabial (see Carrillo de Espinoza, 1974, fig. 4). No consistent or substantive differences in either scutellation or color pattern were noted between the Ancash and Lima Department series. *Sibynomorphus williamsi* shows typical patterns of sexual dimorphism for colubrids. In comparison to females, male *S. williamsi* have significantly fewer ventrals (t = 4.560, df = 13, p < 0.001), significantly more subcaudals (t = 4.365, df = 12, p < 0.01), and greater relative tail lengths (Table 1).

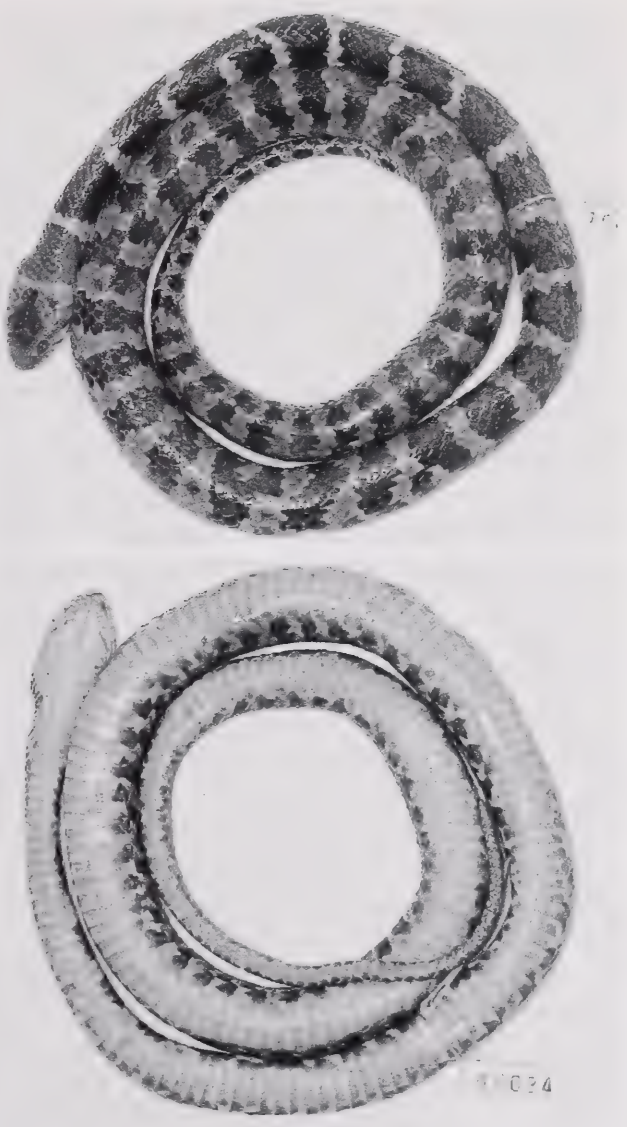


Figure 42. *Sibynomorphus williamsi.* Dorsal and ventral views of a specimen from Lima Department, MUSM 10034. Female, 531 mm SVL.

Color in Life. Unknown. In a relatively recently preserved specimen (MUSM 10034; Fig. 42) the dorsal crossbands are blackish and the interspaces are medium brown with darker brown spots and stippling. The venter is grayish brown, invested with dark grayish irregular markings across each ventral plate.

Color in Preservative. Sibynomorphus williamsi exhibits a consistent color pattern. The dorsum is strongly crossbanded anteriorly, although the bands tend to

break up into dorsal and lateral blotches, sometimes offset, on the posterior half to two-thirds of the body. The first dorsal crossband extends well up onto the wide part of the head in most specimens (Figs. 41, 42). At their widest point (dorsal half), individual crossbands are 6 to 9 dorsal scale rows wide on the anterior part of the body, reducing to 3 or 4 rows wide posteriorly. Ventrally, individual crossbands are 2 to 4 rows wide, and they extend onto the lateral edges (up to approximately one-third) of the ventral plates. The interspaces are very narrow (1 or 2 scale rows wide) the length of the body. The total number of crossbands is 35–48. The dorsal crossbands and interspaces are highly contrasting in most specimens, apparently very dark brown or black in life with much paler interspaces. Ventral patterns of the specimens examined were of three forms: (1) pale whitish with fine dark peppering; (2) rather dusky, especially posteriorly; or (3) whitish or dusky with a posterior series of large rounded or squarish spots on the lateral edges of the ventral scales. Occasionally dark pigment was concentrated in narrow lines across the belly, creating a ladder-like appearance.

The head of *Sibynomorphus williamsi* is brown to grayish with blackish markings. Usually some of the labial scale sutures are lined with black and often irregular dark spots are present on the top and sides of the head, especially the parietal scales.

The color pattern of the two smallest individuals, MUSM 3400 (243 mm total length, 198 mm SVL) and MUSM 2867 (199 mm total length, 159 mm SVL), is similar to that of adults, which indicates that little, if any, ontogenetic change in color pattern occurs. The venter of these specimens is very dusky and with a dark ladder-like pattern formed by a dark irregular line across each ventral. The tops of their heads are also very dark.

Etymology. Sibynomorphus williamsi was named for Ernest E. Williams, former curator of herpetology and professor of biology at the Museum of Comparative Zoology, Harvard University.

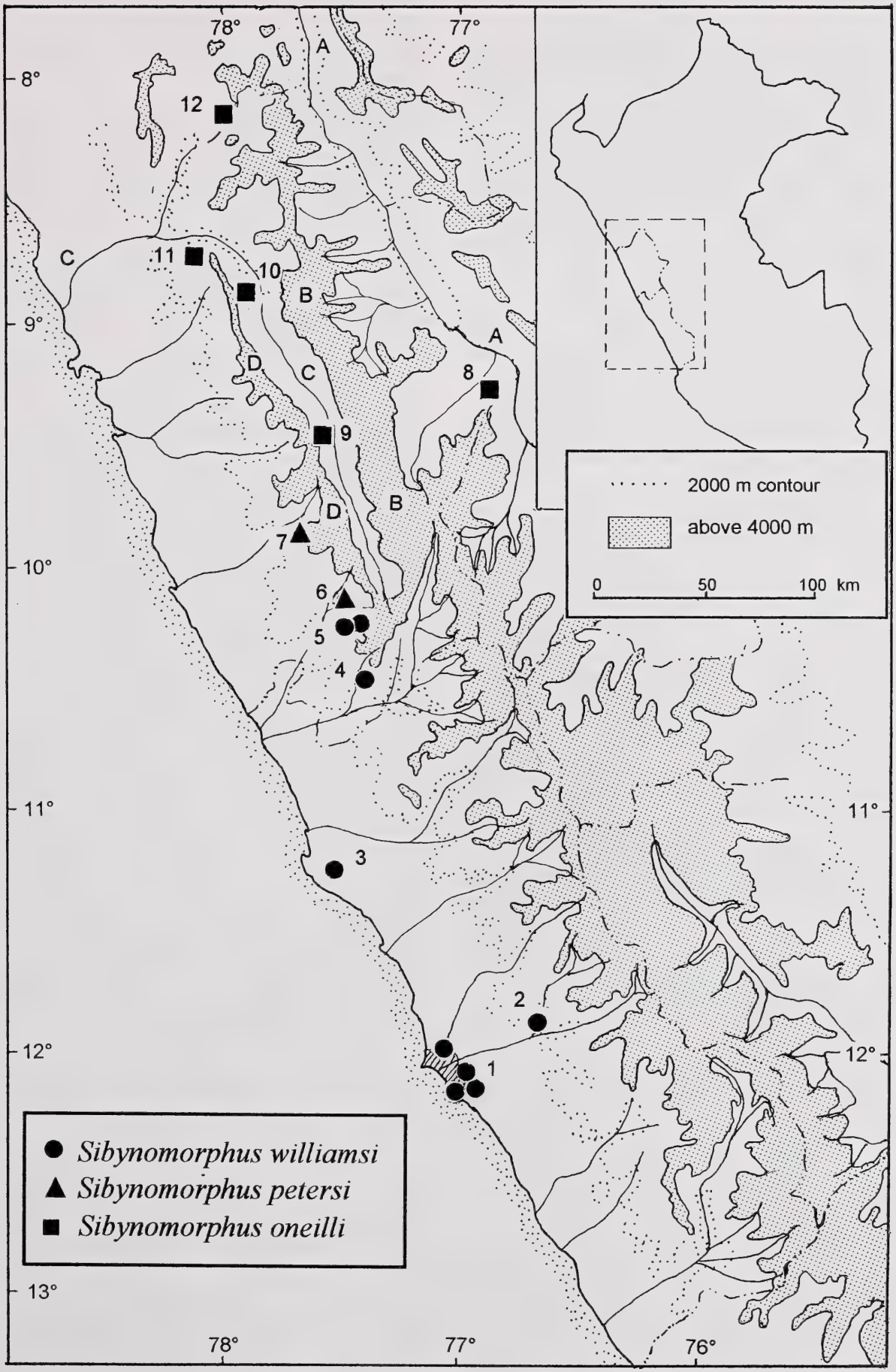
Hemipenis

The following description of the hemipenis of *Sibynomorphus williamsi* is based on the fully everted right organ of the holotype (MUSM 2170); a sketch of the organ was given in the original description (Carrillo de Espinoza, 1974). Total length of the organ 12 mm, bilobed distally for about 1.5 mm.

The hemipenis is slightly bilobed, fully capitate, and with the sulcus spermaticus dividing within the capitulum. The capitulum is set off from the proximal portion of the organ by a well-developed capitular groove. Calyces bearing fleshy papillae ornament the capitulum, but the papillae on the more proximal calyces are spinulate (i.e., have mineralized tips). The sulcus spermaticus divides within the proximal edge of the capitulum and its branches are centrolineal, but distally they pass to the lateral edges of the hemipenial lobes and end at their peripheral distal tips. Proximal to the capitulum is a central section ornamented all around the organ with three to four rows of stout spines. On the asulcate side of the hemipenis is a pair of enlarged spines just proximal to the midsection battery. The basal area below the central spinose section is ornamented with mi-

→

Figure 43. Distributions of *Sibynomorphus williamsi, S. petersi,* and *S. oneilli* in Lima and Ancash Departments, Peru, and adjacent La Libertad Department (locality 12 only). Inset shows the area covered by the larger map (outlined department boundaries are Lima to the south, Ancash to the north). Numbers refer to specimen localities and letters to physical features as follows: **Localities**: ***S. williamsi***: (1) Lima and vicinity: Canto Grande, Lomas de Atocongo, Lomas de Lurín, Jicamarca (type locality), Lomas de Pachacamac; (2) Santa Eulalia; (3) Lomas de Lachay; (4) Huanchay; (5) Yumpe (west) and Huayllacayán (east). ***Sibynomorphus petersi***: (6) Cajacay; (7) Malvas. ***Sibynomorphus oneilli***: (8) Yuracyacu; (9) Huaráz; (10) Huaylas; (11) Hacienda Santa Rosa; (12) Hacienda Ticapampa. **Physical features:** (A) Río Marañón; (B) Cordillera Blanca; (C) Río Santa; (D) Cordillera Negra.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10
11
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2000 m contour
above 4000 m
0
50
100 km
Sibynomorphus williamsi
Sibynomorphus petersi
Sibynomorphus oneilli

nute spines. A large basal nude pocket is present on the lateral surface of the organ, but is positioned almost on the asulcate side (i.e., it seems displaced far more toward the asulcate side of the hemipenis than in other species of *Sibynomorphus*). The pocket is 5.5 mm long and has a lobe at its distal end on the asulcate edge and a large spine at the distal end on the sulcate edge.

Distribution and Natural History

Sibynomorphus williamsi is known from coastal "lomas formations" from the vicinity of Lima north to the Lomas de Lachay, from the Andean foothills east of Lima, and from the Andean slopes of southern Ancash Department, Peru (Fig. 43). The known localities span 10 m to at least 2,990 m, but possibly as high as 3,626 m elevation—an extraordinary elevational range matched in few other snakes of which I am aware. The uncertainty in the upper elevational extent is based on specimens from Huayllacayán, Ancash Department, which could have come from lower elevations than the town itself (see footnote 27). However, there is a dichotomy in the elevational range of localities in Lima Department (10–1,036 m) compared with Ancash Department (1,857–?3,626 m). This might reflect either collection biases or environmental differences, but the absence of information on microhabitats or capture circumstances for *Sibynomorphus williamsi* precludes adequate evaluation.

The new records of *Sibynomorphus williamsi* in the Andean foothills and slopes are significant in showing that the species is not restricted to the coastal lomas formations but could have a broader distribution in the Peruvian coastal region and western Andean slopes. Given the extreme environmental conditions that pertain to much of the Peruvian coastal region, a snake such as *S. williamsi* might be infrequently encountered on the surface and could be overlooked through much of the region. Perhaps significantly, many specimens have come from the heavily populated region around Lima where chance encounters are more likely to record the species' presence.

No detailed observations seem to have been recorded for the circumstances of capture for any specimen of *Sibynomorphus williamsi*. The lomas formations, from which some specimens have come (e.g., the lomas of Lurín, Jicamarca, Pachacamac, and Lachay), are plant communities with a highly endemic flora characteristic of the Peruvian and Chilean coastal region (Rundel et al., 1991). These communities develop where there is sufficient topographic relief to intercept the low, dense clouds characteristic of the winter months, thus providing local mesic environments in this otherwise arid region. The formations from the vicinity of Lima and north are floristically among the most diverse lomas because of the increased moisture in this part of the coast compared to farther south. Fog drip at the Lomas de Lachay, from which *S. williamsi* is known, can reach nearly 700 mm per year (Rundel et al., 1991), which is far more than the amount of actual precipitation. Plant communities at Lachay are a diverse assemblage of herbaceous and semiwoody vascular plants, lichens, terrestrial and arboreal bromeliads, and dense stands of small trees with abundant epiphytes (mosses, lichens, ferns) (Rundel et al., 1991: 32). The topography interacts with the prevailing climate to produce a wide array of microenvironmental conditions, including moist woody ravines, lichen-covered rocky terrain, and sandy shrub habitats. Whether *S. williamsi* is restricted to particular microhabitats within this region is unknown. Also, the Lomas de Lachay are topographically and environmentally more diverse than some other lomas localities for *S. williamsi* (at Lachay the lomas reach nearly 1,000 m elevation). For example, the Lomas de Lurín and Lomas de Pachacamac are of much lower relief and with much simpler and more xeric vegetation communities.

Referring to localities in the vicinity of Lima from which the type series was obtained, Carrillo de Espinoza (1974: 5) stat-

ed that *Sibynomorphus williamsi* was "a species adapted to a xerophytic environment where *Tillandsias* and other deciduous plants grow; of nocturnal habits, possibly semiarboreal because of the compressed nature of its body." She did not elaborate on the observations suggesting nocturnal habits. One locality for *S. williamsi,* Santa Eulalia (Lima Department, 1,036 m), has been characterized as a semidesert (Koepcke, 1961: 35).

Because they are above the level of interception of the winter clouds and fogs characteristic of the Peruvian coast, the localities for *Sibynomorphus williamsi* in Ancash Department (Fig. 43) are notably more arid than the localities at lower elevations in Lima Department. The region has been characterized as montane or bush steppe (Koepcke, 1961; Lehr et al., 2002).

Three specimens from Lima Department with dates of collection were taken in January, February, and October. Six specimens from Ancash Department were collected in February, March, or April. These months, particularly January–April, correspond to the warmer, drier months along the central coastal region of Peru. Dense clouds form along the Peruvian coast from May to October, often with a ceiling of only 150–300 m (Rundel et al., 1991: 9), and cool weather prevails.

One female (MUSM 10034, month of collection not recorded; 531 mm SVL; Fig. 42), contained six eggs, as determined by palpation through the body wall. The smallest individual, MUSM 2867 (157 mm SVL) was collected 9 January 1978.

Leptognathus atypicus Cope, 1874: Incertae Sedis

Leptognathus atypicus Cope, 1874a: 65–66. Holotype unknown. Type locality: "some portion of the Peruvian Andes, from an elevation of twelve thousand feet."

Pseudopareas atypicus: Boulenger, 1896: 463. Werner, 1922: 200.

Sibynomorphus turgidus (part): Amaral, "1929"a [1930]: 33. Peters, 1960: 158, 1965: 13. Peters and Orejas-Miranda, 1970: 278.

The identity of *Leptognathus atypicus* Cope (1874a) has not been conclusively resolved. Neither Peters (1960: 160) nor I located its holotype in the Academy of Natural Sciences of Philadelphia, and it is not among the Cope types acquired by the American Museum of Natural History (Charles W. Myers, personal communication, 1998; see Myers 1982: footnote 7) or the National Museum of Natural History (Cochran, 1961).

Cope's description of *Leptognathus atypicus* in its entirety follows (Cope, 1874a: 65–66):

> Belonging to sec[tion] vi of my monograph of this genus [Cope, 1868: 107–108], that is, with smooth equal scales, and short geneials separated by but one pair of labials from the symphyseals. The body is rather stout, and, unlike most of the genus, nearly cylindric; the neck is not contracted, but the head is wide and flat, and the muzzle short. Scales rather wide; in fifteen rows. Rostral plate subtriangular; a subquadrate loreal; no preocular; postoculars 2; temporals 2 × 3. Frontal and parietals broad and short, the latter truncate. Superior labials six, eye over third and fourth, fifth and sixth elongate. Inferior labials ten, mostly transverse; four pairs of geneials, all except the first broader than long. Tail short, m. .047 in length, from a total of m. .243.
>
> Color pale, with black transverse spots, which are wide anteriorly (the second covers seven transverse rows of scales) and become gradually narrower, having a width of only two cross-rows on the hinder part of the body. Posteriorly their lateral ends are broken off, and alternate with the dorsal portion. A few small blotches on the ends of the gastrosteges.

The description is cursory, even for Cope. For example, he reported neither ventral nor subcaudal counts. Several characters (15 [midbody] scale rows, a rather stout, cylindrical body, a short muzzle, a loreal but no preocular, and a pale dorsum with wide black blotches anteriorly, narrower posteriorly) suggest a species of *Sibynomorphus,* but it is conceivable that it could also be a species of *Dipsas.* Cope's (1868) concept of *Leptognathus* included species now apportioned among *Dipsas, Sibon, Sibynomorphus,* and *Tropidodipsas,* and his "sections" of the genus were not based on characters now considered to be systematically informative, that is, "smooth equal scales, and

short geneials separated by but one pair of labials from the symphyseals [= mental scale]."

Amaral ("1929"a [1930]: 33) considered *Leptognathus atypicus* identical to *Sibynomorphus turgidus,* and Peters (1960: 158) formally placed it in the synonymy of *S. turgidus,* where it has remained since (e.g., Peters and Orejas-Miranda, 1970). Both authors were perhaps guided by Cope's referral of the species to his "section vi" of *Leptognathus,* which, at the time *L. atypicus* was described, included only *S. turgidus* (Cope, 1868: 108). Peters (1960: 160) noted that the differences between *S. turgidus* and the type of *L. atypicus* as described by Cope, particularly labial counts, appeared as variants within his sample of *S. turgidus.* Peters (1960: 160) also questioned Cope's locality because of the high elevation (3,660 m), which was perhaps understandable because the only montane species of *Sibynomorphus* known at the time, *S. vagus,* was known only from <2,000 m elevation.

Nonetheless, because scutellation and color patterns within this group of snakes are highly variable, Cope's brief description precludes a rigorous determination of the identity of *Leptognathus atypicus.* For example, with little amplification, the characters given by Cope also describe *Sibynormorphus oneilli, S. oligozonatus,* and *S. williamsi,* which were unknown to Peters, and these are more logical on geographic grounds than *S. turgidus.* The known upper elevational limits for these species are, respectively, about 3,500, 2,250, and (possibly) 3,600 m (see previous species accounts). One character in Cope's description, six supralabials with the third and fourth touching the eye, is uniquely shared by *S. oligozonatus* and *S. williamsi* among the northern species of *Sibynomorphus* (Table 1). Given the lack of details in Cope's description, the identity of *L. atypicus* will remain questionable unless the type is rediscovered.

I see no reason to question the type locality of *Leptognathus atypicus* as Peters did, although the elevation (3,660 m) is exceptionally high for a species of *Sibynomorphus* or the related genus *Dipsas.* Nonetheless, we still have much to learn about snake distributions in the Andes. For example, the discovery of a new population of *S. oneilli* extended the known elevational range of that species from 1,645 m to over 3,000 m (Rossman and Kizirian, 1993), and *S. williamsi* might occur well over 3,000 m (but see footnote 27).

Ancillary information in Cope's description lend credibility to the locality data. Cope (1874a) stated that the type of *L. atypicus* was presented to the ANSP "along with two fishes." Cope (1874a) described one of the fishes as *Protistius semotilus* (now *Basilichthys semotilus*) and stated that the other was *Trichomycterus dispar* (Tschudi). The holotype of *Protistius semotilus* is still extant (ANSP fish collection 14404), and both species of fish occur in the Andes of Peru. Thus, unless there was a mislabeling or mix-up before these specimens were presented to Cope, it seems likely that the type of *L. atypicus* is also from Peru.

Other circumstantial details suggest, but cannot prove, that Peru might be the origin of *Leptognathus atypicus.* Cope's work on the South American herpetofauna in the 1870s was dominated by the collections of the naturalist James Orton (1830–1877), primarily from Peru. Orton's second expedition in 1873 traversed the Peruvian Andes, including a "side excursion" to Lake Titicaca (Orton, 1875: xiv). Indeed, Cope (1874a: 70–72) included an appendix describing two reptiles denoted explicitly as sent by Orton, and a paper later the same year (Cope, 1874b) described the bulk of Orton's 1873 collections. In addition to the holotype of *Protistius semotilus,* the ANSP fish collection has two specimens of *Trichomycterus dispar* collected by Orton in 1873 at Tinta (Cuzco Department; ANSP 21251, 21355), which could well be the specimens of that species to which Cope referred (Cope, 1874a: 66) (one reading of the expression "two fishes"

is "two kinds, or species" of fishes, rather than two specimens). *Trichomycterus dispar* is not mentioned in the later paper covering most of the fish collection (Cope, 1874b). It is plausible, and perhaps likely, that the holotype of *L. atypicus* was sent to Cope by Orton and that it was obtained on his 1873 expedition to Peru.

HEMIPENIAL MORPHOLOGY IN *SIBYNOMORPHUS* AND OTHER DIPSADINI

As outlined in the following section, I consider the Dipsadini to comprise species in four nominal genera of Neotropical molluscivores: *Dipsas, Sibon, Sibynomorphus,* and *Tropidodipsas.* These are part of a larger clade, the Dipsadinae (sensu Zaher, 1999), essentially the Central American xenodontine clade of Cadle (1984a,b, 1985) with slightly different composition and many taxa listed "incertae sedis" by Zaher (1999). This is not equivalent to the Dipsadinae of Peters (1960), a much smaller clade whose composition is discussed in the next section. As part of Dipsadinae, *Sibynomorphus,* along with species of several other genera (e.g., *Dipsas, Atractus, Leptodeira,* and *Imantodes*), is a South American representative of a clade with a great diversity of species throughout tropical Mesoamerica.

The Dipsadinae has been characterized on the basis of hemipenial synapomorphies. I here summarize the morphology of the hemipenes of *Sibynomorphus,* as gleaned from the previous species accounts, put their variation in the context of other Dipsadinae and Dipsadini, and characterize interspecific variation in hemipenial morphology among species of *Sibynomorphus.* Myers and Cadle (1994) suggested three hemipenial characters as synapomorphies of Dipsadinae, despite some variation within this group and convergent occurrences in other clades of colubrids (Zaher, 1999): (1) unicapitation, (2) either unilobed or slightly bilobed, and (3) sulcus spermaticus dividing distally within the capitulum.

Hemipenes of at least 27 species of Dipsadini, including species of all four genera, have been described (Cadle, 2005; Cadle and Myers, 2003, and herein), although the descriptions vary in the degree of detail presented. Nonetheless, as inferred from these published descriptions and illustrations, hemipenes of the Dipsadini are very similar in ornamentation. Cadle and Myers (2003: 14–15) briefly reviewed these descriptions, described the organs of *Dipsas nicholsi* and *D. andiana,* and corrected a few observations in previously published descriptions (see also Cadle, 2005). Hemipenes of Dipsadini include the following characters in addition to those considered synapomorphies of Dipsadinae: (1) calyces with well-developed papillae ornamenting the capitulum (the papillae on the proximal calyces are spinulate); (2) a well-developed capitular groove; (3) a battery of enlarged spines of varying width (generally three to four rows of spines across but varying from one to five) encircling the hemipenial body proximal to the capitulum; (4) an exceptionally long nude pocket extending from the base of the hemipenis to, or nearly to, the battery of spines around the midsection; and (5) usually two or more basal spines that are larger than, and separated from, spines in the midsection battery. Proximal to the battery of enlarged spines on the midsection, hemipenes of Dipsadini are ornamented with minute spines overall. A brief survey of published descriptions and unpublished data indicates that these characters commonly appear elsewhere among Dipsadinae (e.g., see illustrations of *Rhadinaea* in Myers, 1974), although comparative studies could reveal differences in their manifestation. In the following section, I briefly compare hemipenes of the northern species of *Sibynomorphus* and compare variation in these and other characters in *Sibynomorphus* vis-à-vis other Dipsadini and Dipsadinae.

Comparison of the Hemipenes of *Sibynomorphus*

Hemipenes of the five species of northern *Sibynomorphus* for which the organs

are known (all except *S. oneilli*) are very similar to one another, but they seem to offer few characters that link two or more of the northern species of *Sibynomorphus* to the exclusion of others. References to *Sibynomorphus* in the following discussion refers explicitly to these five northern species only. No other hemipenes of *Sibynomorphus* have been described in sufficient detail to make meaningful comparisons. Cei (1993) and Scrocchi et al. (1993) briefly described organs of several southern species.

(1) Bilobation and Proportions of the Hemipenial Body. The organs are nonbilobed (*S. petersi*) or slightly bilobed. The bilobation is greatest in *S. williamsi* and *S. vagus* (approximately 12–13% bilobed compared with <7% in *S. vagrans* and *S. oligozonatus*). The degree of bilobation varies somewhat among species of Dipsadini, as seen from published illustrations of various species of *Dipsas, Sibon,* and *Tropidodipsas* (reviewed by Cadle and Myers, 2003). However, no species of Dipsadini seems to have more than slight bilobation, and that exhibited by *S. williamsi* and *S. vagus* is about as much as has been observed in any species; Porto and Fernandes (1996) illustrate the hemipenis of *D. neivai,* which shows a similar degree of bilobation.

The capitulum composes a large proportion of the hemipenial body in *Sibynomorphus.* In the species examined herein, the capitulum is approximately 50% or more of the body on the sulcate surface (see Figs. 32, 39). A review of notes and hemipenial illustrations in the literature suggests that this could be proportionally large compared with many other Dipsadinae. Further comparative studies are needed to determine whether useful systematic variation in this character exists.

(2) Orientation of the Sulcus Spermaticus. In hemipenes of all species of *Sibynomorphus* described herein, the orientation of branches of the sulcus spermaticus is centrolineal, but their distal tips pass somewhat to the outer edges of the lobes (Figs. 32, 39). In typical centrolineal sulci, the branches "diverge moderately and extend in relatively straight lines, to lie on the same side . . . as the forking point of the sulcus" (Myers and Campbell, 1981: 16). Thus, the condition in *Sibynomorphus* might be perceived as somewhat intermediate between centrolineal and centrifugal orientation (in which the branches diverge greatly, to lie ultimately on opposite, lateral sides of the organ; Myers and Campbell, 1981: 16). This somewhat intermediate condition has been noted in other Dipsadini, including *Dipsas andiana* and *D. nicholsi* (Cadle and Myers, 2003). However, Zaher et al. (2005: 22, fig. 3) described a seemingly very similar orientation of the sulcus spermaticus of *Atractus albuquerquei* as "centrifugal."

Published illustrations of hemipenes of other Dipsadini generally show more consistently centrolineal orientations of the sulcus (Kofron, 1982, 1985a,b), although the branches in *D. neivai* appear to pass somewhat lateral as well (Porto and Fernandes, 1996). The tips of the sulcus spermaticus in the five species of *Sibynomorphus* surveyed end at the lateral edges of the lobe(s) rather than passing to the apical surface of the organ, i.e., to the center of the lobe(s). This condition is similar to that in *D. andiana* and *D. nicholsi* (see Cadle and Myers, 2003: fig. 6, bottom).

(3) Spines Encircling the Hemipenial Body. A regular array of spines completely encircles the hemipenial body just proximal to the capitulum in *Sibynomorphus.* The array is consistently about three rows across, although in *S. vagrans* and *S. vagus* the array broadened to about four rows on the asulcate surface. This battery of spines appears to be a constant feature of hemipenes of Dipsadini, but its width varies from one to five rows in published descriptions (Cadle and Myers, 2003; Kofron, 1987). Observations of *Dipsas oreas* (Cadle, 2005: 108) suggest that this battery can vary in width intraspecifically so that too much should probably not be made of interspecific differences on the basis of ob-

servations of few organs. The size of the spines in the midsection battery varies within *Sibynomorphus* and in other Dipsadini (e.g., *Sibon*; Kofron, 1982, 1985b, 1987, 1988), but these are usually distinctly smaller than the enlarged basal spines characteristics of Dipsadini (character 7 below).

(4) Presence and Size of the Basal Nude Pocket. One unusual feature of hemipenes of Dipsadini seems to be the exceptional size of the basal nude pocket, which is commonly 30% or more of the overall length of everted organs. It extends from the base of the organ to, or almost to, the encircling battery of spines. The extremes as currently known are in species of *Sibynomorphus,* in which the pockets in everted organs of *S. vagus* and *S. vagrans* are 23% and 26% of the hemipenial length, respectively, whereas in *S. williamsi,* the pocket is 46% of the everted organ length. Too much should not be made of these quantitative comparisons until some potential sources of variation in relative pocket size are investigated more thoroughly, including the effects of preservation, overall size, and degree of inflation. Current data suggest that the size of the nude pocket relative to hemipenial size is greater in inverted organs than in everted ones. For example, the relative pocket size in inverted versus everted hemipenes of *S. vagrans* and *S. vagus,* as described herein, are 32% versus 26% and 30% versus 23%, respectively.

Some published descriptions of hemipenes of Dipsadini fail to mention a basal nude pocket but Cadle and Myers (2003: 15) pointed out that the pocket had probably been overlooked in several of these, as examination of additional specimens showed the pocket to be present. Peters (1960) did not mention the pocket at all in his brief characterizations of the hemipenes of *Dipsas, Sibon,* and *Sibynomorphus.* I now suspect that the pocket has been overlooked in all species of Dipsadini in which the pocket was not reported in published descriptions (e.g., MacCulloch and Lathrop, 2004; McCranie, 2006; Passos et al., 2005; Scrocchi et al., 1993; additional citations and observations in Cadle and Myers, 2003: 15) and that this character will prove universal in Dipsadini. Cadle and Myers (2003: footnote 7) pointed out that longitudinal folds on the base of the hemipenial body might need to be separated with fine forceps or needles to visualize the pocket and that the pocket is especially difficult to demonstrate if the organ is tied off with thread. I encourage workers to make efforts to verify the existence of the pocket during study of hemipenes. The exceptional size of the pocket in Dipsadini might prove to be another synapomorphy of the clade, although more extensive quantitative comparisons need to be made, as well as a broader survey to verify the presence or absence of a nude pocket in other Dipsadinae.

A basal nude pocket is present in some other Dipsadinae (and many other colubrids), including *Geophis* (Downs, 1967; Myers, 2003); *Imantodes* (Myers, 1982); the *Rhadinaea flavilata, R. godmani,* and *R. vermiculaticeps* groups (Myers, 1974); and *Atractus* (Hoogmoed, 1980; Myers and Schargel, 2006; Savage, 1960; Zaher et al., 2005). Moreover, judging from my experience with dipsadines, the failure to mention a nude pocket in published descriptions cannot be taken as definitive evidence of its absence. For example, photographs of hemipenes of three species of *Leptodeira* appear to show a basal nude pocket (Duellman, 1958: pls. 26, 27), even though pockets were not mentioned in any descriptions (the presence of pockets is indicated by what appears to be a deep furrow bordered by lobes such as commonly ornament the nude pockets in other snakes, as seen especially in Duellman's pl. 26, no. 1). Thus, the taxonomic distribution of basal nude pockets among Dipsadinae might be broader than indicated by a literature survey of hemipenial descriptions. The exceptional length of the nude pocket in Dipsadini is seemingly approached in some species of the genus

Atractus, in which the pocket in inverted organs of some species extends distally to the level of the division of the sulcus spermaticus (Hoogmoed, 1980; Savage, 1960). On the other hand, Zaher et al. (2005) described the nude pocket on the hemipenis of *A. albuquerquei* as "small."

(5) Position of the Basal Nude Pocket. The pocket is consistently on the lateral surface of the hemipenial body in *Sibynomorphus* (i.e., about midway between the sulcate and asulcate surfaces, as discussed in *Methods*), although in *S. williamsi* it seemed farther displaced toward the asulcate surface than in the other species. Cadle and Myers (2003) reported variation in the position of the basal nude pocket in different species of Dipsadini, with all species examined except two having the pocket positioned laterally as in *Sibynomorphus.* Cadle and Myers (2003) reported that in one specimen each of *Dipsas variegata* and *Sibon nebulatus,* the nude pocket was on the asulcate surface of the hemipenis. A review of my original notes suggests that this might have been overstated because the notes indicate that the pocket in these two specimens "is offset from the midpoint of the asulcate side"—a loose description that might be no different from the laterally positioned pockets observed in other Dipsadini. Cadle (2005) and Cadle and Myers (2003) reported a laterally positioned nude pocket in five other species of *Dipsas* and *Sibon.*

Nonetheless, Kofron (1982, 1985b, 1987, 1988) described the nude pocket in several species of *Sibon* and *Dipsas* as an "asulcate pocket" (species for which he used this descriptor include *S. annuliferus, S. carri, S. fasciatus fasciatus, S. fischeri fischeri, S. fischeri kidderi, S. sartorii, D. brevifacies,* and *D. gaigeae*). However, different observers could apply terminology differently, so this apparent variation should be verified before acceptance at face value. In addition, the manner of preparation or differential inflation of this pliant tissue could affect the position of the nude pocket, resulting in apparent intra- or interspecific variation.

(6) Lobes Associated with the Nude Pocket. The nude pockets in *Sibynomorphus oligozonatus* and *S. vagrans* are bordered on each side by a prominent lobe. The lobe on the asulcate edge of the pocket (i.e., toward the asulcate side of the organ) is larger than the lobe toward the sulcate side. The nude pockets in *S. petersi, S. vagus,* and *S. williamsi* are bordered only by a single lobe on the asulcate edge of the pocket. The lobes are usually near the midpoint of the pocket, but at least in *S. williamsi,* the single lobe was near the distal end. Other Dipsadini show variation in this feature as well: *Dipsas nicholsi* and *D. elegans* have a single lobe on the asulcate edge of the pocket; *D. andiana, D. oreas,* and *D. ellipsifera* have a lobe on each side of the pocket (Cadle, 2005; Cadle and Myers, 2003). In *D. ellipsifera,* the lobes are asymmetrical, with the asulcate lobe being larger than the lobe on the sulcate edge. In dipsadine species with two lobes, the lobe on the asulcate edge is often (? usually) larger than the sulcate lobe, and in species in which only one lobe is present, it consistently seems to be the lobe on the asulcate edge. One or more lobes are commonly associated with hemipenial nude pockets in diverse colubrids having a pocket, and the variation could merit further study.

(7) Enlarged Spines on the Hemipenial Body. In everted hemipenes of the species of *Sibynomorphus* described herein, usually two enlarged spines are present on the asulcate side of the organ below, or at the lower edge of, the encircling battery of spines (sometimes more closely associated with the nude pocket, as in *S. petersi*). In addition, another enlarged spine is present on the distal sulcate edge of the nude pocket. In everted organs, these enlarged spines are often, but not universally, clearly separated by a gap from spines in the midsection battery (in inverted hemipenes the enlarged basal spines are generally not clearly separated from spines in the mid-

section battery). Basal spines are generally notably enlarged compared with spines in the midsection battery, but because spines in the battery vary in size (see character 3 above), enlarged basal spines might not be clearly differentiated if there is not a distinct gap separating the basal spines from the battery (I recorded only a single asulcate spine in *S. vagus,* but that could reflect lesser size distinction in the specimen studied between the enlarged basal spines and those of the midsection).

Enlarged basal asulcate spines are frequently present in other Dipsadini judging from figures and descriptions in the literature (e.g., Kofron, 1982, 1985b, 1987; Porto and Fernandes, 1996), but their number varies. For example, Cadle and Myers (2003) reported 2–4 basal spines in *Dipsas nicholsi* (the number varied among specimens), and in a single organ of *D. andiana,* two enlarged basal spines were present in addition to two enlarged spines associated with the distal asulcate edge of the nude pocket (Cadle and Myers, 2003).

The position of the enlarged basal spines varies somewhat, sometimes being more closely associated with the asulcate edge of the nude pocket and in other cases deployed more clearly on the asulcate side of the organ. This variation could reflect differences in hemipenial preparations (e.g., degree of inflation) or their interpretation, but side-by-side comparisons are needed to verify the consistency of these placements. Moreover, Kofron (1985b) reported that the largest spines in the hemipenis of *Sibon carri* were on the sulcate side of the organ.

(8) Miscellaneous Variation. A few unique or unusual hemipenial characters seemingly pertain to individual species of *Sibynomorphus.* The proximal calyces on the hemipenis of *S. petersi* have weakly developed longitudinal walls, giving the appearance of weakly developed flounces on the proximal edge of the capitulum. This morphology is observed occasionally in colubrids, but I am unaware of other species of Dipsadini with incipient flounces. Species of *Sibynomorphus* (and other Dipsadini; see Cadle and Myers, 2003) vary in a few characters such as spine form (e.g., narrow, relatively straight, and hooked only at their tips in *S. vagrans,* compared with relatively robust and strongly hooked in the other species). The calycular papillae vary in length (e.g., longer in *S. vagrans* than in *S. vagus*), but I have been unable to compare organs of most species simultaneously to objectify these differences. Similarly, my notes indicate a distinct fringe of mineralized spinules or small spines on the proximal edge of the capitulum in *S. oligozonatus* and *S. vagrans.*

SIBYNOMORPHUS AND THE DIPSADINI: DIRECTIONS FOR FURTHER RESEARCH

In this paper, I lay some foundation for future work on *Sibynomorphus* by outlining patterns of variation in the Ecuadorian and Peruvian species, thus providing a framework for interpreting new specimens or data from northwestern South America. The systematic conclusions herein should facilitate a better understanding of the relationship (if any) between the *Sibynomorphus* species of Ecuador and Peru, and those of southern South America. Detailed comparisons of the two sets of species remain for future research.

Recent studies on the systematics and biology of Neotropical molluscivores (e.g., Cadle, 2005; Cadle and Myers, 2003; Fernandes, 1995; Fernandes et al., 2002; this paper) have already refined knowledge of the species-level taxonomy and distributions since the group was last reviewed (Peters, 1960). Nevertheless, much remains to be done. With over 60 species (including nominal taxa in the genera *Dipsas, Sibon, Sibynomorphus,* and *Tropidodipsas,* as outlined by Peters and Orejas-Miranda, 1970, and subsequently described species), the Neotropical molluscivores comprise a highly diverse and tightly knit clade of Neotropical snakes (see ensuing discussion). More changes in

the understanding of species limits can be expected. Moreover, the phylogenetic relationships among the species have been controversial (Fernandes, 1995; Kofron, 1985a; Wallach, 1995). Although this study does not attempt to address broader relationships among species of molluscivores (beyond comparisons among the species covered herein), the summaries of character variation contained herein should ultimately be useful to that end. In the following sections, I outline some of the problems as I see them and pose some questions for future research on this group.

The Systematics of Dipsadini—An Outline of Some Problems

The Content of Dipsadini. Within Dipsadinae, *Sibynomorphus* has long been considered closely related to the genera *Dipsas, Sibon,* and *Tropidodipsas* (e.g., Dunn, 1935, 1951), with the exception that Peters (1960) did not consider *Tropidodipsas* in his review of "Dipsadinae." Peters did not elaborate on his exclusion of *Tropidodipsas,* although he may have been following Boulenger (1894, 1896), who included *Tropidodipsas* as then known in the Colubrinae and recognized the Amblycephalidae for Asian molluscivorous colubrids and most species of *Dipsas, Sibynomorphus,* and *Sibon* then known. Zaher (1999) referred to the putative clade comprising *Dipsas, Sibon, Sibynomorphus,* and *Tropidodipsas* as Dipsadini and I follow that usage here.

Underwood (1967) observed that *Dipsas, Sibon,* and *Sibynomorphus* have an extensive tracheal lung, which is lacking in *Tropidodipsas.* Wallach (1995) interpreted the presence of a tracheal lung as a derived character of *Dipsas, Sibon,* and *Sibynomorphus,* and explicitly excluded *Tropidodipsas* from the Dipsadini because it lacks this derived character.[17] However, that evidence could equally well be taken as a synapomorphy of *Dipsas, Sibon,* and *Sibynomorphus* within Dipsadini (including *Tropidodipsas*), rather than a reason for excluding *Tropidodipsas* from Dipsadini. At the least, *Tropidodipsas* shares with *Dipsas, Sibon,* and *Sibynomorphus* a behavioral propensity to consume gastropods as nearly the sole constituent of its diet (Cadle and Greene, 1993). Wallach (1995) viewed the dietary specialization as a derived feature linking *Tropidodipsas* with the other dipsadine genera but felt that, by extension, "a case could be made for the gastropod diet as a synapomorphy of the Dipsadini plus Pareatini [*Aplopeltura* and *Pareas*]" (Wallach, 1995: 479). However, the Pareatini lack the hemipenial and other synapomorphies of Dipsadinae (see Zaher, 1999), the broader clade to which the Dipsadini belongs, and moreover, some specializations for molluscivory in the two groups differ in details of anatomy (Brongersma, 1956, 1958; Zaher, 1999: 20). Those differences indicate that the dietary specializations of the Pareatini and Dipsadini are convergent in these groups.

Thus, there is no reason *not* to consider "molluscivory" a synapomorphy of *Dipsas, Sibon, Sibynomorphus,* and *Tropidodipsas* within the Dipsadinae. The behavioral trait for dietary specialization can also be viewed as a proxy for an array of other traits associated with the physical ability to subdue these prey (head musculoskeletal system, head glands, dentition, head scalation; Peters, 1960) and, very likely, biochemical traits associated with the sensory apparatus involved in prey detection and recognition. For these reasons, I suggest that the Dipsadini be defined to include *Tropidodipsas* along with *Dipsas, Sibon,*

[17] Wallach (1995: 479) also noted three characters of visceral topography that "separate the dipsadines from *Tropidodipsas,*" but it was not clear whether these were derived characters. One of these, the position of the posterior tip of the lung, does not seem to clearly differentiate *Tropidodipsas* from some species of each of the other three genera of Dipsadini (Wallach, 1995: table 1), contrary to the text discussion (Wallach, 1995: 479).

and *Sibynomorphus,* as already advocated by Zaher (1999). Although the morphological traits associated with molluscivory have been repeatedly described in general terms for the Dipsadini or portions thereof (e.g., Dunn, 1951; Peters, 1960: 15–19; Scott, 1967), a modern analytical study of their distribution across species is needed. When incorporated into a formal phylogenetic analysis of Dipsadini, this approach should yield valuable insights into the evolution of feeding specializations within a speciose clade.

Sibynomorphus *in the Context of Other Dipsadini: Is* Sibynomorphus *Monophyletic?* Species of Dipsadini have had an especially unsettled generic taxonomy, as examination of the synonymy of virtually any species will readily show (e.g., Cadle, 2005; Cadle and Myers, 2003). Useful reviews of the taxonomy are Peters (1960: 12–15 and, with special reference to *Sibynomorphus,* 142–144), Smith and Taylor (1945: 49), and Kofron (1985a: 85–86). The current generic taxonomy derives from Peters (1960), notwithstanding some disagreement about the recognition or composition of the included genera (e.g., Fernandes, 1995; Kofron, 1985a; Wallach, 1995). The generic taxonomy should be revised as understanding of relationships among species of Dipsadini improves, but that understanding is, as yet, elusive. Despite many suggested revisions of the generic taxonomy of Dipsadini, methodological or sampling problems pertain to many previous considerations of the issue. Here I outline some of the issues and point toward ways of possible resolution.

Kofron (1985a) synonymized *Tropidodipsas* with *Sibon* on the basis that species of both genera shared a "unique" posterolateral process on the maxilla (compared with its absence in three species of *Dipsas* he examined); the process was preceded by a notch on the dorsal surface of the bone. However, Scott (1967) had reported presence of the maxillary process in *D. gracilis,* and Boulenger's (1896: 461) illustration of the skull of *Dipsas indica* shows a maxillary notch similar to that portrayed by Kofron (1985a: figs. 1, 2). As discussed above, Wallach (1995) resurrected *Tropidodipsas* on the basis of tracheal lung and other visceral characteristics. These studies have contributed substantially to our knowledge of morphological characteristics in species of Dipsadini. However, the species and character sampling for a diverse clade such as Dipsadini has generally been less than desirable in previous broad taxonomic studies; they have essentially taken an "exemplar" approach, wherein a few species are taken to represent many others. For example, Kofron (1985a) used three species to represent *Dipsas* in his comparisons despite conflicting character data already reported for another (Scott, 1967). Despite the rarity of some dipsadines in collections, my impression is that there is much more material available than has yet been incorporated into broader phylogenetic studies. I encourage more comprehensive surveys of species and characters to flesh out the character distributions already noted in previous studies (Fernandes, 1995; Kofron, 1985a; Wallach, 1995).

Since Peters' (1960) review, *Sibynomorphus* has been understood to comprise more "generalized" or terrestrial members of the Dipsadini. Species of *Sibynomorphus* lack highly compressed bodies, enlarged heads and eyes, elongate bodies and tails, and enlarged vertebral scale rows (characters generally associated with arboreality in snakes). However, these characters also apply to most species of the related genus *Tropidodipsas* (sensu Wallach, 1995; see also Cadle, 1984a; Kofron, 1985a), a diverse assemblage of Mexican and Central American species that Peters (1960) did not consider in his revision of the Dipsadinae (= Dipsadini of present understanding, i.e., the genera *Dipsas, Sibon, Sibynomorphus,* and *Tropidodipsas*). Although *Sibynomorphus* are primarily terrestrial snakes, observations suggest that at least some species occasionally climb: *S. ventrimaculatus* climbs a meter

or more (Cechin and Oliveira, 2003) and *S. neuwiedii* and *S. mikanii* have been described as "semi-arboreal" (Sazima, 1992) or "terrestrial/arboreal" (Rodrigues, 2003).

Furthermore, Peters (1960: 19) had pointed out that "one of the greatest obstructions to a satisfactory analysis of snakes of [the tribe Dipsadini] is that species with nearly every combination of . . . characters [associated with mollusc-feeding and arboreality] can be found." In view of this, Peters' (1960: 12–19, 141–145) discussion of generic delimitations within this group seems arbitrary. Cadle and Myers (2003) noted that most species of Dipsadini for which any data are available share some unusual characters of the hemipenes (e.g., very large basal nude pockets) and defensive behaviors, but none of these characters appeared to be restricted to particular genera of this group. The possibility should be addressed whether the species of *Sibynomorphus* are a phenotypically similar, but not monophyletic, set of species whose peculiar distribution is purely artifactual because of an erroneous understanding of relationships. Only a broader study of phylogeny at the species level among snakes of the tribe Dipsadini can resolve this issue.

Compared with *Sibon* and *Tropidodipsas, Sibynomorphus* shares with *Dipsas* some derived characters of the gular region: notably, the shape of the chin shields (squarish or polygonal rather than elongate and narrow), often more than two pairs of chin shields, and absence of the mental groove. *Sibon* and *Tropidodipsas* have corresponding character states that might be considered plesiomorphic because they are widespread among Dipsadinae and other colubrids: one or (usually) two pairs of narrow, elongate chin shields similar to those typically found in colubrids, and a mental groove (in *Sibon* often only the anterior chin shields are conspicuously elongate).

Sibynomorphus and *Dipsas* also are usually said to share a suite of musculoskeletal features of the head associated with molluscivory that are more derived than those of *Sibon* and *Tropidodipsas* (Kofron, 1985a; Peters, 1960; Savage, 2002), including an inward-turned maxilla with medially directed teeth, pterygoids that are parallel (as opposed to diverging), pterygoids with a flat ventral surface (as opposed to having a central fossa), mandibles bowed in a vertical plane, and a pivot joint between the dentary and compound bone of the lower jaw (Kofron, 1985a: 88; Peters, 1960). In reality, these characters have not been investigated in most species of either genus. For example, with the exception of a few skull characters described for *S. lavillai* (Scrocchi et al., 1993), the nature of these characters is unknown in the five species of *Sibynomorphus* described since 1970, and at least some of the characters have been reported in species of *Sibon* and *Tropidodipsas* (e.g., Fernandes, 1995; Scott, 1967). Newly described species of *Sibynomorphus* have been referred to the genus by a combination of "key" external and dentition characters usually used in generic recognition (e.g., Peters and Orejas-Miranda, 1970).

Over the years, several authors have recommended synonymizing *Sibynomorphus* with *Dipsas* (e.g., Brongersma, 1958; Kofron, 1990: 220; Parker, 1926: 206; Smith and Taylor, 1945: 49), a name that Boulenger (1896), among others, applied to a single species, *D. indica.* The two genera were traditionally distinguished by the presence (*Sibynomorphus*) or absence (*Dipsas*) of pterygoid teeth until Parker (1926) indicated that interspecific variation in this character was nearly continuous. Parker also reported intraspecific variation in the number of pterygoid teeth within "*Sibynomorphus oreas*" (= *Dipsas oreas*). That evidence is a red herring, however, inasmuch as the BMNH specimens Parker cited belong to two different species (Cadle, 2005: 114). Nonetheless, Peters' (1960) data show that absence of pterygoid teeth is approached in very few species of Dipsadini (e.g., *D. indica, D. variegata*) and that many species of *Dipsas* (sensu Peters, 1960) have as many, or more, pterygoid teeth as species of *Sibynomorphus.*

Peters' (1960: 144) justification for maintaining *Sibynomorphus* distinct from *Dipsas* seems particularly arbitrary: "I agree in part with Parker [1926]. I feel that the generic distinction between the many species formerly included in the genus *Sibynomorphus* and . . . the genus *Dipsas* is not valid, but I use the name *Sibynomorphus* in an extremely restricted sense, confining it to the stem forms found in southern Brazil and neighboring countries." It is unclear how the two species of *Sibynomorphus* from northern Peru known at the time, *S. vagrans* and *S. vagus,* fit into this concept. Peters (1960) provided little in the way of differential diagnoses for these two genera other than a few external characteristics in his "Key to the Genera" (Peters, 1960: 19), e.g., body form, head and eye size, relative enlargement of the vertebral scale row. Evidence for the monophyly of *Sibynomorphus* is thus particularly weak.

In an as yet unpublished doctoral dissertation dealing with a broad sampling of Dipsadinae, Fernandes (1995) argued that *Sibynomorphus* should be synonymized with *Dipsas* because his phylogenetic analysis recovered one character purportedly shared by two species of *Sibynomorphus* (*S. neuwiedii* and *S. ventrimaculatus*) and two species of the *Dipsas catesbyi* group (*D. catesbyi* and *D. pavonina*) to the exclusion of other *Dipsas* (seven additional species included in the analysis). It is beyond the scope of this report to present an extended critique of Fernandes' (1995) study, but taxon and character sampling issues alone suggest that synonymizing the two genera is premature. Only two of 12 species of *Sibynomorphus* (*S. neuwiedii* and *S. ventrimaculatus*) and nine of 30+ species of *Dipsas* were included in the taxon sampling for formal phylogenetic analysis (Fernandes, 1995: figs. 7, 8). None of the northern species of *Sibynomorphus* were investigated. The derived character linking the two species of *Sibynomorphus* and two members of the *D. catesbyi* group (*D. catesbyi* and *D. pavonina*) was an enlarged L-shaped Harderian gland. Although this character state was coded as present in *S. neuwiedii* (Fernandes, 1995: table 3), the list of material studied does not indicate that the head glands of this species were investigated (Fernandes, 1995: appendix B), and the character was scored as unknown in two of the nine species of *Dipsas* examined. Furthermore, the type species of *Sibynomorphus* is *S. mikanii* Schlegel, a species that Fernandes (1995) did not include in the formal phylogenetic analysis, so from a purely nomenclatural viewpoint, synonymizing *Sibynomorphus* with *Dipsas* on that basis entails some unwarranted assumptions about the phylogenetic unity of *Sibynomorphus.*

In addition to these issues, some analytical aspects of Fernandes' (1995) study need more careful consideration before making further changes in the generic taxonomy of these snakes. These include more thorough evaluation of intraspecific character variation, character scorings, and more robust tree searching and evaluation methods. For example, intraspecific variability (or error in character scoring) in the purported character linking *Sibynomorphus* with *Dipsas catesbyi* and *D. pavonina* is suggested by Brongersma's (1958: 11) observation that the Harderian gland is enlarged in *D. catesbyi* but "small" in *D. indica* and *D. pavonina,* contrary to Fernandes' (1995) finding.

Even as some authors have called for synonymizing *Sibynomorphus* with *Dipsas,* no one has specifically addressed whether *Sibynomorphus* itself (sensu Peters, 1960, and including subsequently described species) is monophyletic. Although quantification and comprehensive comparisons at the species level are needed, for present purposes, *Sibynomorphus* is distinguished from *Dipsas* by lacking physical characteristics associated with arboreality (highly compressed and attenuate body, prehensile tail, and different head, eye, and tail proportions; Peters, 1960). Many more characters should be investigated in

a broad spectrum of species of *Sibynomorphus* and *Dipsas* from throughout their geographic ranges.

A search should also be made for new characters that could potentially inform phylogenetic studies of Dipsadini. Among these are perhaps patterns of sexual dimorphism. Cadle (2005: 77) noted that several species of *Dipsas* had unusual patterns of sexual dimorphism, including one species (*D. elegans*) in which males had greater numbers of ventral plates than females (i.e., the reverse of the common pattern in colubrids); two other species, *D. ellipsifera* and *D. oreas,* lacked sexual dimorphism in ventral plate numbers, which is also an uncommon pattern. A subsequent review of Peters' (1956: fig. 12) data for *D. catesbyi* suggested that the unusual pattern observed in *D. elegans* pertained to *D. catesbyi* as well, and perusal of several papers on other Dipsadini hinted at possible unusual patterns of sexual dimorphism in other species. These include considerable overlap in the ventral and subcaudal counts of male and female *Sibon annulifera, S. sartorii sartorii, S. dimidiata,* and *S. sanniola* (Kofron, 1988, 1990). Unfortunately, Kofron presented only ranges for most comparisons, and he combined male and female counts in other papers so that it is impossible to discern any trends (a practice followed also by Savage and McDiarmid, 1992). However, Kofron (1990) reported mean values for male and female ventrals in *S. s. sanniola* as 155 and 153, respectively. This suggests little or no sexual dimorphism in ventral counts for this species (the character ranges of males and females were nearly identical as well).

In contrast to these unusual patterns, the Ecuadorian and Peruvian species of *Sibynomorphus* are not unusual with respect to patterns of sexual dimorphism: they show the patterns most common in colubrids generally. Whether the southern species of *Sibynomorphus* show typical or unusual patterns of sexual dimorphism is not clear (e.g., data for *S. lavillai* from Scrocchi et al. [1993] showed little difference between males and females for ventral counts). Nonetheless, this character might provide an additional distinction between some species of *Sibynomorphus* and some *Dipsas.* Broader and more quantitative surveys could prove fruitful.

Sibynomorphus (or a part thereof) could thus be plesiomorphic relative to *Dipsas* in terms of ecomorphological characters associated with arboreality and with respect to patterns of sexual dimorphism. These plesiomorphic characters in *Sibynomorphus* do not support the monophyly of *Sibynomorphus* per se, but they do provide a differential diagnosis from *Dipsas* until more detailed studies are conducted. Further changes to the taxonomy of these snakes should be commensurate with an increase in understanding of a suite of characters and their variation across a broad sampling of nominal taxa of Dipsadini—something that has been lacking in previous examinations of the generic taxonomy.

The Peculiar Distribution of Sibynomorphus. Certainly one outstanding feature of *Sibynomorphus* as currently understood is its odd distribution, which is unlike most other Neotropical reptiles and amphibians (Fig. 44). Lest this peculiarity be construed as "evidence" for the nonmonophyly of *Sibynomorphus,* it is worth briefly comparing the distribution to other South American species. The six species of *Sibynomorphus* that form the focus of this report (the "northern species" in the following discussion) are distributed in southern Ecuador and the northern half of Peru, and these are species of the Pacific versant (coast, Andean slopes, and western inter-Andean valleys) or of the eastern inter-Andean valleys on the Amazonian versant (Río Marañón and its affluents, Río Huancabamba and Río Chotano). Then follows a broad geographic gap before the genus appears again in the dry woodlands of southern Bolivia (Fugler and Cabot, 1995; Fugler and De la Riva, 1990) and the Brazilian state of Mato Grosso, whence it is broadly distributed south of the main

Figure 44. The widely disjunct distribution of species of *Sibynomorphus* in western Peru and Ecuador, and south of the Amazon basin. The distribution of the "northern" species is compiled from records herein. The distribution of the "southern" species is compiled from Peters (1960), Cei (1993), Leynaud and Bucher (1999), and various other faunal works. Question marks indicate my inability to find reliable records through a large part of the Brazilian cerrado. Similarly, the distribution might be more continuous in the borderlands between Bolivia, Paraguay, and Argentina.

course of the Amazon. About 1,500 km (straight line distance) separates the closest points in the two parts of the distribution, not to mention the rugged terrain of the Andes and parts of forested lowland Amazonia, where no species of *Sibynomorphus* seems to occur.

South of the Amazon, species of *Sibynomorphus* (the "southern species") occur in an extraordinary range of major habitats, including cerrado, caatinga, Atlantic forest, chaco, pantanal, and dry deciduous woodlands (Brites and Bauab, 1988; Cei, 1993; Leynaud and Bucher, 1999; Marques et al., 2000; Norman, 1994; Peters, 1960; Rodrigues, 2003; Vanzolini, 1948). There seem to be no definite records from within the Amazonian forest. The collective distributions of the southern species of *Sibynomorphus* are remarkably similar to that of the colubrid snake genus *Psomophis,* except that *Psomophis* is conspicuously absent from the Atlantic Forest and caatinga (Myers and Cadle, 1994) (Rodrigues [2003] described the presence of *S. mikanii* in caatinga as relictual). Apart from *S. vagrans* and coastal populations of *S. williamsi,* the northern species of *Sibynomorphus* are montane species and occur at higher elevations than are known for any of the southern species.

With the exception of *Sibynomorphus neuwiedii,* which is apparently restricted to forested regions of the Atlantic Forest biome (Hoge et al., "1978/1979" [1981]: 177), southern species of *Sibynomorphus* primarily occur in relatively open habitats, often with reduced rainfall. The ecological (particularly microhabitat) distribution of the northern species of *Sibynomorphus* is not well known, but subhumid to arid environments prevail in this region. Localities for most northern species, as documented in the natural history sections of the species accounts, are referred to frequently by descriptors such as arid habitats with cacti, semiarid brushland, dry deciduous forests, thorn scrub, arid rain shadow valleys, and montane steppe. Nonetheless, a few records for *S. petersi* (e.g., Río Zaña Study Site, Bosque Cachil, Canchaque, Río Chotano valley) suggest that this species, at least, occurs in the dry/humid forest ecotone, if not actually within humid montane forests (see species account), and other species might occur in more mesic areas, such as riparian habitats, than their general habitat associations might imply.

Species of *Sibynomorphus* are not unique among Dipsadini in their occurrence in subhumid to xeric habitats. A few species of the other genera occur in habitats such as dry deciduous forests, thorn forests, or deserts (e.g., *Dipsas brevifacies* and *D. gaigeae, Sibon sanniola, Tropido-*

dipsas annulifera). Nevertheless, species of *Dipsas, Sibon,* and *Tropidodipsas* overwhelmingly inhabit more mesic to humid environments than species of *Sibynomorphus.* In the case of broad macrosympatry between *D. oreas* and *S. petersi* (see its species account) in southern Ecuador and northern Peru, these two species might be segregated by habitat, with *S. petersi* occurring in more arid environments than *D. oreas* (see footnote 7).

The disjunct distribution of *Sibynomorphus* is unusual but not without parallels. The Pacific coastal and western Andean region of northern Peru and Ecuador (the generalized distribution of the northern species of *Sibynomorphus*) harbors a distinctive and largely endemic herpetofauna. Few components of this fauna have been subjected to phylogenetic studies, but three examples illustrate parallels with the distribution of *Sibynomorphus* (Fig. 45).

In the frog genus *Ceratophrys* ("Leptodactylidae" or Ceratophryidae), *C. stolzmanni* (southwestern Ecuador/northwestern Peru) is the sister taxon to *C. calcarata–C. cornuta* (Caribbean Colombia/Venezuela and the Amazon basin), and these three species, composing the subgenus *Stombus,* are the sister group to the subgenus *Ceratophrys* (Lynch, 1982), which occurs in forested and nonforested habitats from southern Bolivia and northern Argentina east throughout southern Brazil (Fig. 45B). Thus, apart from the existence of a widespread Amazonian species (*C. cornuta*) and a northern South American species (*C. calcarata*), the distributional relationships of the western South American species, *C. stolzmanni,* are similar to distribution patterns portrayed by species of *Sibynomorphus* as that genus is presently understood.

The lizard *Ctenoblepharys* (Liolaemidae; Fig. 45C) is endemic to loose sand habitats of coastal central Peru. It is the sister group to *Phymaturus* + *Liolaemus* of the southern Andes and Pacific coast (Argentina–Chile), and cis-Andean South America from Argentina to southern Brazil (Espinoza et al., 2004; Etheridge, 1995). Thus, an area cladogram for Liolaemidae is similar to that of *Sibynomorphus* (Fig. 45A), with the additional geographic components of the southern Andes and coast.

Finally, among tropidurid lizards, *Microlophus* (Fig. 45D), from western Ecuador and Peru (including inter-Andean Marañón valley of northern Peru and the Galapagos Islands), is the sister group to other tropidurid genera (*Tropidurus, Plica, Uracentron, Eurolophosaurus,* and *Strobilurus*) (Frost et al., 2001), whose geographic distribution encompasses Amazonia, the Guayanan region, and virtually all of austral South America (i.e., south of the Amazon basin). Again, Amazonian and Guayanan taxa represent geographic components not found in *Sibynomorphus.* Although the examples in Figure 45 seem most similar to the distribution of *Sibynomorphus,* other possible examples might be found in genera such as *Stenocercus* (Tropiduridae) and *Philodryas* (Colubridae), which have coastal/Andean components in Peru, Ecuador, or both and which are broadly distributed east of the Andes and in austral South America.

Each of these examples includes geographic components (Amazonia, southern Andes and southern Pacific coast, northern South America) not known in *Sibynomorphus.* Nonetheless, a complete phylogenetic analysis of Dipsadini at the species level might eventually show that these "missing" geographic components are represented by species whose relationship to *Sibynomorphus* is not yet demonstrated (i.e., species of *Dipsas*). This is especially true given that monophyly of *Sibynomorphus* is not yet demonstrated, and its relationship to other Dipsadini (particularly the diverse array of Amazonian and northern South American *Dipsas*) is presently murky.

Moreover, the cladograms in Figure 45 illustrate two alternative area relationships among species of western Ecuador/Peru, austral South America, and Amazonia. In *Ceratophrys* (Fig. 45B) the western Ec-

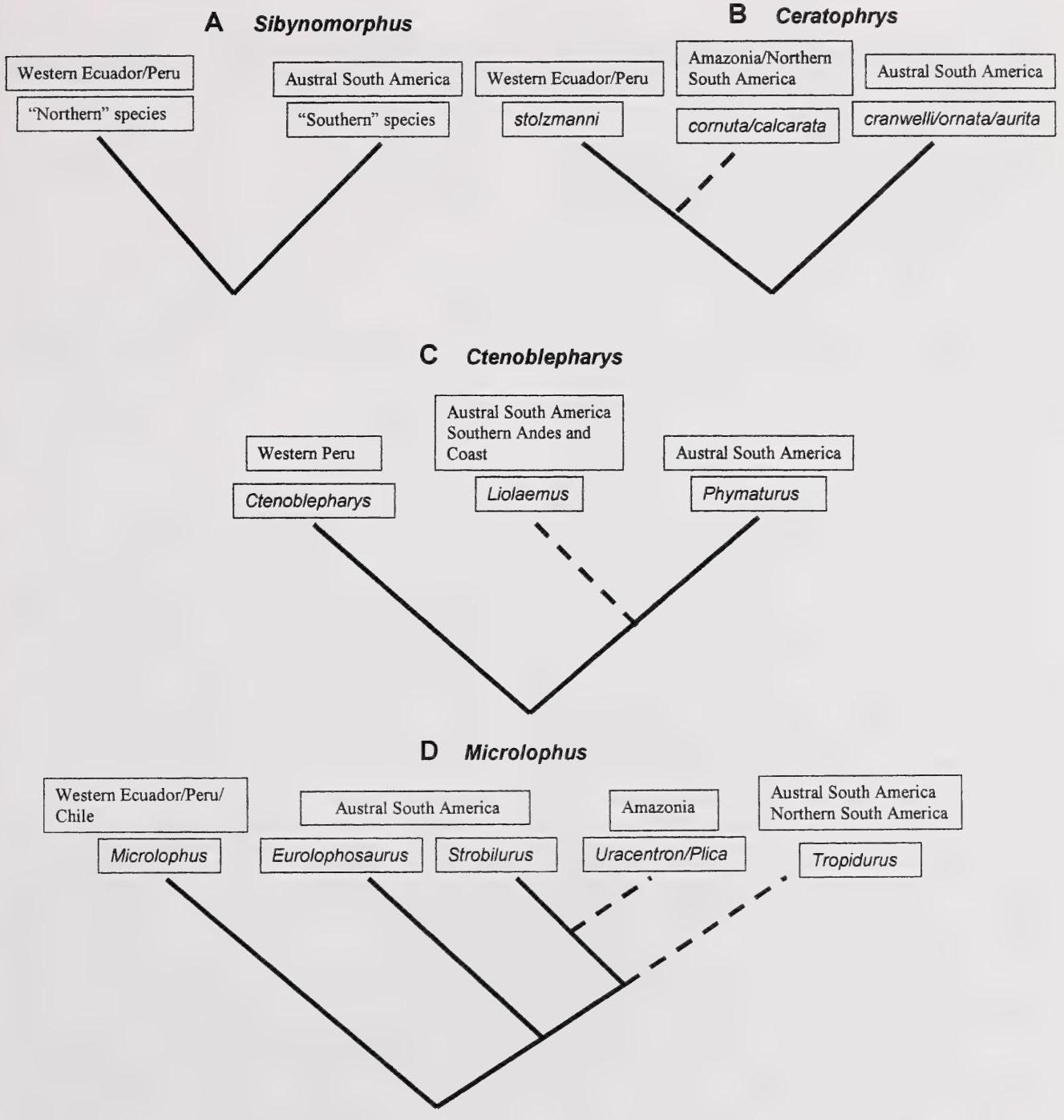

Figure 45. Area cladograms illustrating geographic components (areas of endemism) shared between *Sibynomorphus* and other taxa of western South America. "Austral South America" here refers to all of cis-Andean South America south of Amazonia; the exact area delimited varies somewhat in each case (see discussion and references in the text). Solid lines in the cladograms indicate shared geographic components. Dashed lines indicate one or more geographic components not present in *Sibynomorphus*. (A) Geographic components in *Sibynomorphus*. Neither the monophyly of the genus itself nor its geographic components ("northern" and "southern" species groups) is strongly supported (see text). (B) Geographic components in the frog *Ceratophrys* (Leptodactylidae or Ceratophryidae). (C) Geographic components in the lizard *Ctenoblepharys* (Liolaemidae). (D) Geographic components in the lizard *Microlophus* and related lizard genera (Tropiduridae).

uador/Peru taxon is most closely related to the Amazonian species, whereas in *Microlophus* (Fig. 45D), the Amazonian taxa are more closely related to the austral South American taxa. For *Ctenoblepharys* (Fig. 45C), the area cladogram is identical with that of *Sibynomorphus* (i.e., no Amazonian component is present) except that species

of *Liolaemus* also occur in the southern Andes and the southern Chilean coast, geographic components also unknown in *Sibynomorphus.*

Depending on how the phylogenetic relationships among the northern and southern species of *Sibynomorphus* and the species of *Dipsas* are ultimately resolved, the area cladogram for *Sibynomorphus* could resemble any of the examples in Figure 45 or more complex geographic relationships. For example, three possible resolutions of the area cladogram for *Sibynomorphus* are shown in Figure 46, in which dashed lines to the geographic component "Amazonia" represent as yet undemonstrated relationships of the northern (western Ecuador/Peru; Fig. 46A) or southern (austral South America) species of *Sibynomorphus* (Fig. 46B). The former resolution is compatible with the area cladogram for *Ceratophrys* (Fig. 45B), and the latter is compatible with the area cladogram for *Microlophus* (Fig. 45D). Many more complex resolutions are possible, of which the example in Figure 46C is but one example (i.e., the northern and southern species of *Sibynomorphus* are each independently related to different species groups of Amazonian *Dipsas*). The example in Figure 46C would imply that *Sibynomorphus* as it is currently known is polyphyletic.

The possibilities outlined in Figure 46 are speculative, but they indicate ways in which some outstanding phylogenetic and biogeographic enigmas concerning *Sibynomorphus* might ultimately be resolved. Figure 46 also provides guidelines for constructing any rigorous test for relationships between *Sibynomorphus* or any of its geographic components and other Dipsadini. At the least, northern and southern species of *Sibynomorphus* must be included in analyses, preferably with a broad taxonomic and geographic representation of South American species of *Dipsas* as well. Unless tests are constructed such that these alternatives can potentially be discerned, we are left with more ambiguity than clarity.

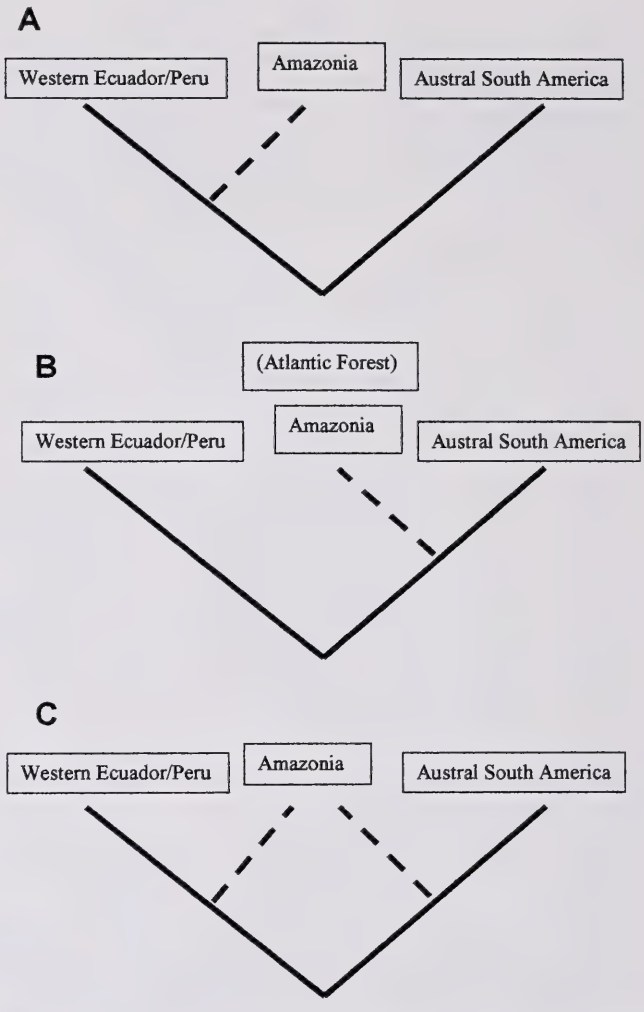

Figure 46. Examples of possible resolutions of "missing" geographic components in the area cladogram of *Sibynomorphus* (Fig. 45). These area cladograms assume a complex relationship between geographic components of *Sibynomorphus* and species of *Dipsas,* which currently is speculative (see text). (A) Resolution corresponding to the area cladogram of *Ceratophrys* (Fig. 45B). (B) Resolution corresponding to the area cladogram of *Microlophus* (Fig. 45D); a possible alternative is indicated by the additional geographic component "Atlantic Forest," which is a component of "Austral South America" used in Figures 45 and 46. (C) A more complex scenario in which the northern and southern species of *Sibynomorphus* are each related to different species of *Dipsas* in Amazonia, which implies polyphyly of *Sibynomorphus* as currently understood. Many more resolutions of these area cladograms are possible, but all depend on the precise relationship among the northern and southern species of *Sibynomorphus* and other species of South American Dipsadini. These relationships are largely unexplored.

Research Needs on the Northern Species of *Sibynomorphus*

More Field Work and Collections are Needed. Several topics addressed in this study need additional research based on

more samples than currently exist. Systematic studies of some tropical snakes are hampered because few specimens from widely scattered localities are available, and species of *Sibynomorphus* in Ecuador and Peru are no exceptions. In extreme cases, species can be represented by unique or nearly unique specimens as, for example, in the species of "rare snakes" of the genera *Geophis* and *Atractus* studied by Myers (2003). None of the species of *Sibynomorphus* considered herein is as absolutely rare as the species considered by Myers (2003). However, interpreting patterns of variation and inferring species limits was difficult in several cases because of inferred intrapopulational or geographic variation combined with few specimens sampled across the complex terrain of the Andes. Even with the new material reported herein, one of the species is known from only four specimens, and three species are known from three or fewer localities. Great variability in systematic characters has been documented within species of *Sibynomorphus* (Rossman and Kizirian, 1993; this study) and related genera (e.g., *Dipsas*; Cadle, 2005; Cadle and Myers, 2003). The variation occurs at several levels (individual variation within populations, sexual dimorphism, and geographic variation among populations) and with respect to scutellation and color patterns. Teasing apart the sources of variation in taxa represented by few specimens is particularly difficult.

Because of the variability of informative systematic characters within and between population samples and few specimens spread over a topographically and environmentally diverse region of South America, the available material of Ecuadorian and Peruvian *Sibynomorphus* is insufficient to fully clarify their systematics. Thus, the identity of some populations proved difficult to resolve. Because of the extensive variation in characteristics such as color patterns and scutellation, the species limits recognized herein should be reviewed as more material and denser geographic sampling become available. In particular, the concepts of *Sibynomorphus oligozonatus, S. petersi,* and *S. oneilli* need reassessment. Full characterization of *S. oligozonatus* is hampered by few specimens and rather large disparity among specimens in a few characters, such as ventral counts within males and between males and females.

For *Sibynomorphus petersi* and *S. oneilli,* the problems of species limits have more to do with character variation among localities. The Peruvian samples of *S. petersi* are heterogeneous in color patterns among themselves and compared with Ecuadorian samples. Ecuadorian specimens tend to be more homogeneous in color patterns, but they also form a more cohesive geographical unit than Peruvian samples, which are spread in a linear array along the western Andean front (Fig. 25). For *S. oneilli,* the problem is that the type specimen differs in several characters from virtually all other specimens referred to this species, and it is the only specimen currently known from the Cordillera Oriental. Efforts should be made to obtain additional specimens (particularly adults) from the vicinity of the type locality to verify whether the unusual characters of the holotype pertain to this individual or reflect population or regional characteristics.

Additional field work is needed to flesh out the distributions of *Sibynomorphus* in Peru in more detail. In particular, field work at the northern end of the Cordillera Oriental in Peru (east of the Río Marañón in La Libertad, San Martín, and Amazonas Departments) should be undertaken to understand more fully the distribution of *S. oneilli* in this region (currently known only from a single specimen, the holotype, from east of the Río Marañón). Similarly, *S. petersi* is known from a single specimen on the Amazonian versant, and the extent of its distribution east of the continental divide should be established. There is also a broad geographic gap in the distribution

of *S. petersi* on the Pacific versant between southern Ancash Department and the next locality to the north, San Pablo (Cajamarca Department) (Fig. 25). *Sibynomorphus vagus* and *S. vagrans* are known only from single locations, and the latter species has apparently not been collected since Noble collected the type series in 1916, even though it seemed to be common at that time (see species account).

As currently known, the distribution of *Sibynomorphus williamsi* along the Peruvian coast is peculiarly circumscribed. Specimens have been recovered from several localities in the immediate vicinity of Lima and from the relatively well-studied Lomas de Lachay just north of Lima (Fig. 43). The lomas formations extend from northern Chile to northern Peru and, although their general aspect becomes drier from the vicinity of Lima southward, the climate in general for this region is relatively homogeneous (Rundel et al., 1991). Comprehensive field surveys of the lomas formations should reveal whether *S. williamsi* is more broadly distributed in this habitat along the Peruvian coast. These environments have rarely been given attention by zoologists, and new discoveries are likely. (Pearson and Ralph [1978] studied bird, mammal, and lizard communities of a loma in southern Peru, but their sampling protocol was unlikely to reliably sample secretive or highly seasonal snakes.)

A further paradox concerning the distribution of *S. williamsi* concerns its elevational distribution. All initially reported localities were from coastal lomas formations less than 1,000 m in elevation (and all, except the Lomas de Lachay, <300 m) (Carrillo de Espinoza, 1974). The localities in Ancash Department differ in elevation (>1,800 m) and environment (more xeric) from these coastal formations. The breadth of the elevational distribution of *S. williamsi* (10 to perhaps 3,600 m) is extraordinary for a species of snake and invites more detailed distributional studies and population comparisons to determine whether all are, in fact, the same species.[18] In particular, field studies of coastal areas in southern Ancash Department could determine whether the upland populations are linked to any at lower elevations in this region. Similarly, additional study of the Andean foothills east of Lima should determine whether *S. williamsi* occurs more generally in this area (the species is currently known only from one inland locality in Lima Department, Santa Eulalia).

Currently, the only known case of sympatry among any of the northern species of *Sibynomorphus* is the presence of *S. petersi* and *S. oligozonatus* at their type locality in Azuay Province, Ecuador. It seems likely that these two species are broadly sympatric throughout the highland areas of southern Ecuador and (possibly) northern Peru (Figs. 7, 25). Potential areas of sympatry for species of *Sibynomorphus* in Peru include southern Ancash Department, where three species (*S. oneilli, S. petersi,* and *S. williamsi*) occur in close proximity (Fig. 43). Further field work is needed to determine whether there is microsympatry among these species and, if so, to what extent their resource use patterns are similar.

Systematic and Phylogenetic Issues. Much work remains to be done on the systematics of *Sibynomorphus* in the broad sense and achieving a well-supported phylogenetic hypothesis for its relationships within Dipsadini. Chief among the outstanding questions is whether *Sibynomorphus,* as it has been understood since Peters (1960) (i.e., the northern + southern species), is monophyletic. Fernandes (1995) formalized the suggestion raised many times previously that *Sibynomorphus* stemmed from within *Dipsas,* but the possibility also exists that *Sibynomorphus*

[18] Two other snakes of the Pacific versant also have huge elevational ranges. *Mastigodryas heathii* and *Philodryas simonsii* are known from near sea level. The former ranges to at least 2,500 m and the latter to over 3,000 m in the Andes of northern Peru (Cadle, unpublished data).

is polyphyletic with respect to *Dipsas*. For example, the two geographic units (northern and southern) could be independently related to different clades within *Dipsas* or there could be an even more complex relationship among species of the two genera (see above discussion and Figs. 45 and 46). These are unexplored questions.

This study yielded few clues as to relationships among any of the species reviewed. Three species, *Sibynomorphus oligozonatus, S. williamsi,* and *S. vagrans,* resemble one another in several characters. Their color patterns are less variable intraspecifically, and they are more similar to one another than any of the other three northern species, which are quite variable in color pattern. *Sibynomorphus oligozonatus, S. williamsi,* and *S. vagrans* all have highly contrasting dorsal patterns (bold crossbands on relatively pale ground colors) and relatively unmarked venters compared with *S. oneilli, S. petersi,* and *S. vagus. Sibynomorphus oligozonatus* and *S. williamsi* share some characters that are rare or absent in other species of the genus: (1) They share the uncommon characteristic of having six supralabials with the third and fourth bordering the eye—a characteristic seen elsewhere in some specimens of *S. lavillai* and *S. ventrimaculatus* (Scrocchi et al., 1993), but not among other northern species of *Sibynomorphus* (Table 1). (2) They consistently lack separate preoculars (i.e., the preocular is always fused with the prefrontals in the specimens examined) and have elongate loreal scales. Among the northern species of *Sibynomorphus,* lack of a separate preocular was observed elsewhere only in some specimens of *S. oneilli* but was reported as a consistent feature of *S. mikanii* and the usual condition in *S. ventrimaculatus* (Cei, 1993). (3) They tend to have fewer maxillary teeth than the other northern species. The color patterns of *S. oligozonatus* and *S. williamsi* are similar except for the less distinct bands/blotches on the posterior body of *S. oligozonatus* and its broader anterior crossbands compared with *S. williamsi.*

On the other hand, *Sibynomorphus oligozonatus* shares with *S. vagrans* the presence of two lobes associated with the nude pocket on the hemipenial body (one asulcate lobe in the other northern species). The color patterns of these two species are also very similar, including broad anterior crossbands, less distinct posterior crossbands, and relatively unmarked venters (Figs. 1, 3–6, 28, 29). It is unclear whether any of these similarities among *S. oligozonatus, S. vagrans,* and *S. williamsi* are indicative of close phylogenetic relationships in the absence of broader comparisons. Also, as perceived by Dunn (1923), *S. vagrans* is similar to *S. vagus* in having low ventral counts compared with the other species.

Further comparative studies of all species referred to *Sibynomorphus* are needed, particularly in the context of other Dipsadini. Three of the northern species, *Sibynomorphus oneilli, S. petersi,* and *S. williamsi* attain larger sizes (males, 563–763 mm total length; females, 718–790 mm total length; Table 1) than any of the southern species (generally <500 mm total length in males and females; Cei, 1993; Scrocchi et al., 1993). Intraspecific variation in scutellation is generally much less in *Sibynomorphus* than in *Dipsas* (Peters, 1960; this study; cf. Cadle, 2005; Cadle and Myers, 2003). Such comparative studies should yield insights not only into the systematics of this group, but into aspects of their natural history.

Natural History Studies. The paucity of data on the natural history of all northern species of *Sibynomorphus* is evident from the species accounts contained herein. Microhabitat and behavioral data are almost completely lacking for all species, and only a single dietary record (a gastropod) is available (see *S. oligozonatus*). Two records document predation on *S. petersi* and *S.* cf. *oneilli* by coral snakes (*Micrurus*). Three records document clutch sizes for *S. petersi* (two clutches of five eggs each)

and *S. williamsi* (six eggs), but dates of collection are not available for these specimens, and nothing concerning reproduction is known for the other northern species of *Sibynomorphus*. Most specimens with recorded dates of collection have been obtained in the austral summer (i.e., generally between October and April), although *S. petersi* has also been obtained during the austral winter (June–August) in southern Ecuador. Seasonal activity and reproductive patterns for these species need to be documented with greater precision. The proximity of two species, *S. williamsi* and *S. oneilli*, to major population centers (Lima vs. Huaráz and Cajamarca, respectively), offers significant opportunities for detailed local natural history studies.

Finally, two aspects of variation within *Sibynomorphus* and the Dipsadini deserve further study relative to the natural history of these snakes: color and scales. A puzzling aspect of variation in several species of northern *Sibynomorphus* (*S. oneilli, S. petersi, S. vagus*) is considerable intra- and interpopulational variation in color pattern. Each of these species varies in pattern from relatively unicolor (or finely reticulated or flecked) to strongly banded (see species accounts and illustrations herein). This variation poses a systematic question: Are species limits correctly inferred, and do the color patterns thus truly represent intraspecific variation? Assuming that the answer to the first question is "yes," how is the color pattern variation related to the natural history of the snakes?

Species of Dipsadini are widely suspected to mimic pit vipers in color patterns and behaviors (Greene and McDiarmid, 2005). Such mimicry has been specifically suggested for *Sibynomorphus neuwiedii* (Sazima, 1992), and defensive behaviors similar to that of *S. neuwiedii* have been reported for *S. mikanii* (Cadle and Myers, 2003). Perhaps the extreme pattern polymorphism in several northern species of *Sibynomorphus* is associated with specific and, as yet unknown, defensive behaviors or mimicry systems.

Some northern species of *Sibynomorphus* are known to be regionally sympatric with species of *Bothrops*: *S. oligozonatus* and *S. petersi* with *B. lojanus* and *B. osbornei* in southern Ecuador (Campbell and Lamar, 2004; Parker, 1930, 1932, 1938); *S. oneilli* and *S. williamsi* with *B. pictus, B. roedingeri,* or both in northern and central Peru (inferred from distributions in Campbell and Lamar, 2004). In addition, some of these species of *Bothrops* are highly polymorphic in color and pattern (e.g., *B. pictus*; Campbell and Lamar, 2004). Parallel studies of geographic color pattern variation could shed light on potential mimicry systems in these snakes, as could a study of populations at localities in which high intrapopulational pattern variation has been documented (e.g., *S. oneilli* in the Río Santa valley of Ancash Department, Peru; *S. vagus* from the vicinity of Huancabamba, Piura Department, Peru). Although current evidence suggests that little or no ontogenetic change in color pattern occurs in *Sibynomorphus*, more detailed investigations of this phenomenon should be conducted. Do potential models (*Bothrops*) and mimics (*Sibynomorphus*) undergo parallel ontogenetic color changes, as is known in some other snake mimicry systems (Greene and McDiarmid, 2005)?

A second intriguing aspect of the biology of *Sibynomorphus* and other Dipsadini (particularly *Dipsas*) is the extreme variation in external scalation (Cadle, 2005; Cadle and Myers, 2003; Peters, 1960). The variation in standard scutellation characters, particularly of the head, seems greater than occurs in many other colubrid groups. It calls for study in mechanistic terms (What developmental processes result in the variation?); in functional biology terms (What is the functional significance of the variation?); and in evolutionary terms (What is the phylogenetic distribution and origin of the variation?).

It is tempting to link variability in scu-

tellation to the molluscivorous diet of Dipsadini (and perhaps some correlated changes such as the musculature underlying the temporal scales; see Dunn, 1951). Indeed, the absence of a mental groove and the peculiar form of the chin shields have been linked specifically with the ability to consume gastropods (Gans, 1952: footnote 5; Peters, 1960: 17–18). But that can be only part of the story because *Sibynomorphus* and *Dipsas* are more derived in these two characters than are *Sibon* and *Tropidodipsas* (see above discussion). *Sibynomorphus* itself is less variable in some head scale characters than are at least some *Dipsas* (e.g., scales in the loreal and temporal regions). The variation among species could be related to different functional requirements for different prey, and different species of Dipsadini are already known to have different prey preferences and correlated morphology (e.g., in *Sibynomorphus*; LaPorta-Ferreira et al., 1986; Sazima, 1989). Functional and comparative studies of head scale variation in snakes could shed light on this phenomenon in Dipsadini. A fruitful avenue of research also includes a variational study of the Asian molluscivores (Pareatini). Do their patterns of variation entail the same scales and to the same degree of variation as in Dipsadini? This could suggest insights into how the variation might be related, if at all, to molluscivory in colubrids.

Species of *Sibynomorphus* in Ecuador and Peru offer many opportunities for deepening our understanding of the biology of the South American radiation of Dipsadini. Hopefully, the analyses presented here will stimulate further studies of these snakes to resolve outstanding systematic and phylogenetic questions and will serve as a point of departure for improving knowledge of their natural history.

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SPECIMENS EXAMINED AND LOCALITY RECORDS

AMNH American Museum of Natural History, New York
ANSP Academy of Natural Sciences of Philadelphia
BMNH The Natural History Museum, London
EPN Escuela Politécnica Nacional, Quito, Ecuador
FMNH Field Museum of Natural History, Chicago
KU Museum of Natural History, University of Kansas, Lawrence
MCZ Museum of Comparative Zoology, Harvard University, Cambridge
MUSM Museo de Historia Natural de San Marcos, Lima, Peru
USNM National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Sibynomorphus oligozonatus

ECUADOR: AZUAY: Zhila, Parroquia Oña, Cantón Girón, 2,250 m [03°30′S, 79°12′W],[19] EPN 3612 (holotype). About 6 km airline W Santa Isabel, 1,440 m, Río Jubones drainage [03°16′S, 79°19′W], AMNH 110587. **LOJA:** Catamayo Valley, 30 km W Loja [approximately 04°01′S, 79°20′W], BMNH 1935.11.3.108.

PERU: PIURA: No specific locality, MUSM 2192, 2248.

Sibynomorphus oneilli

PERU: ANCASH: Provincia Antonio Raimondi: Yuracyacu, 3,500 m [09°15′S, 77°01′W[20]], MUSM 3211, 3296, 3303, 3334, 3392, 3448. Huaráz [3,060 m; 09°32′S, 77°32′W], MUSM 3395, 2660. Provincia Huaylas: Huaylas [2,721 m; 08°52′S, 77°54′W], MUSM 2662, 2687, 3089. Provincia Huaylas: Hacienda Santa Rosa, 1,800 m [now Provincia Santa: approximately 08°46′S, 78°08′W [21]], MUSM 2390. **AMAZONAS:** 5,400 ft. (1,646 m) on road between Balsas and Abra Chanchillo [06°49′S, 77°59′W], LSUMZ 33736 (ho-

[19] Coordinates for this locality given by the GeoNet Names Server (03°30′S, 79°12′W) differ from those given in the original description (03°39′45″S, 79°17′26″W). Consultation with several maps suggests that the former are more accurate. The Global Gazetteer gives the elevation of Zhila as 2,818 m.

[20] Instituto Geográfico Militar, Departamento de Ancash, 1:400,000, 1979.

[21] Stiglich (1922) indexes two haciendas in Ancash Department with the name "Santa Rosa": one in the District of Mácate, the other in the District of Pueblo Libre. All of the territory of Pueblo Libre is ≥2,000 m, whereas Mácate has significant area <2,000 m, and I infer this is the Santa Rosa referred to. Mácate has subsequently been incorporated into Santa Province (IGM Departamento de Ancash, 1:400,000, 1979). The coordinates are an approximation on the basis of the closest territory to Mácate that is <2,000 m. MUSM 2390 was collected by Roberto Donoso-Barros, but no date was recorded.

lotype). **Cajamarca:** Abra Gelic, 13 km E Celendín, 3,080 m [06°51′S, 78°08′W], KU 212599. Provincia Cajabamba, 10 km SSE Cajabamba, 2, 900 m [approximately 07°37′S, 78°03′W], KU 212600. Provincia Cajabamba: Cajabamba [2,654 m; 07°37′S, 78°03′W], MUSM 3103. **La Libertab:** Provincia Santiago de Chuco: Hacienda Ticapampa [= Hacienda Ticabamba, Distrito de Mollepata; Stiglich, 1922; approximately 08°11′S, 77°57′W, the coordinates of Mollepata], MUSM 2770.

Sibynomorphus cf. *oneilli*

PERU: "Bellavista," MUSM 2258 (see text discussion at end of species account for *S. vagrans*).

Sibynomorphus petersi

ECUADOR: Azuay: Zhila, Parroquia Oña, Cantón Girón, 2,250 m [03°30′S, 79°12′W; see footnote 19], EPN 2659 (holotype; not seen), 2660 (paratype). **Loja:** Loja City, 2,200 m [04°00′S, 79°13′W], BMNH 1924.6.24.110–111, 1930.1.30.7, 1930.10.12.24–25, 1931.2.12.30–31, BMNH 1933.6.24.110–111. Vicinity of Loja City, 7,280 ft. [2,219 m; 04°00′S, 79°13′W], BMNH 1935.11.3.111. 0.5 km E Loja City on road to Zamora, 6,765 feet [2,063 m; 04°00′S, 79°13′W], USNM 237040. 2 km E Loja, 2,200 m [04°00′S, 79°13′W], KU 121309. 10 km E Loja City [04°00′S, 79°11′W], EPN 4737. Catamayo Valley, 30 km W Loja, 4,780 ft. [1,457 m; 04°01′S, 79°20′W], BMNH 1935.11.3.109–10. 7.3 km N Loja, 2,080 m [03°58′S, 79°13′W], KU 142804. Cantón Saraguro, El Tablón, 03°28′42″S, 79°10′30″W, EPN 1847 (not seen; Orcés and Almendáriz, 1989).

PERU: Ancash: Malvas, 3,120 m [09°55′S, 77°39′W], SMF 80048. Cajacay, 2,599 m [10°09′S, 77°26′W], MUSM 20583 (not seen; Lehr et al., 2002).[22] **Cajamarca:** 3–4 km N Paraguay (along road from Querocoto to Hacienda La Granja), 2,420 m [06°21′S, 79°05′W],[23] MUSM-JEC 12884. Approximately 1 km NE (airline) of Monte Seco on trail between Monte Seco and Chorro Blanco, Río Zaña, 1,250 m [06°51′S, 79°06′W], FMNH 232569. El Chorro, 1 km N (airline) Monte Seco, 1,400 m, Río Zaña, ANSP 31806 (= stomach contents, not separately catalogued, associated with a *Micrurus mertensi* (see Fig. 26). San Pablo [2,400 m; see Cadle, 1998: footnote 6; 07°07′S, 78°50′W], BMNH 1900.3.30.19. Bosque de Cachil, 3 km (airline) SW Contumazá, 2,200–2,400 m [07°23′S, 78°47′W], MCZ 178047. **Piura:** 33 km SW Huancabamba, below (west) crest of the Cordillera Huancabamba ["below camp, ca. 6800 ft" (2,073 m) fide field notes of Richard Thomas; approximately 05°21′S, 79°34′W],[24] LSUMZ 27374.

Sibynomorphus vagrans

PERU: Cajamarca: Bellavista [421 m; 05°37′S, 78°39′W], MCZ 17284 (holotype), 17428, 17436–52 (paratypes).[25]

Sibynomorphus vagus

PERU: [Piura]: Huancabamba [1,929 m; 05°14′S, 79°28′W], MCZ 17420–23,

[22] I assume that the identity of MUSM 20583 is the same as SMF 80048, which I examined. Both specimens are from the same collection and from geographically close localities (see Lehr et al., 2002).

[23] Coordinates derived from 1: 100,000 Carta Nacional Incahuasi, Departamento Cajamarca (IGM, 1965, reprinted 1973).

[24] This locality is roughly equivalent to "Canchaque" or "Cruz Blanca" in some literature on this locality. See footnote 13.

[25] Paratypes of *Sibynomorphus vagrans* comprised 26 specimens (Dunn, 1923), but Barbour and Loveridge (1929) indicated only 23 [*sic*] at that time: MCZ 17430–53 [= 24 specimens]. Several paratypes were exchanged to other collections: Instituto Butantan (17429–30, 17435), University of Illinois Museum of Natural History (17431), Hebrew University of Jerusalem (17432), AMNH (17433, 17453), and the Naturhistorischen Museums in Wien, Austria (17434). These exchanged specimens were not examined for this study.

17425–26[26]; Huancabamba (1,900 m), KU 135180; Huancabamba (1,820 m), KU 219121–22. 5.7 km N Huancabamba on road to Salala, 1,920 m, KU 219123; MUSM 15464–65 (not seen; Rossman and Kizirian, 1993).

Sibynomorphus williamsi

PERU: Ancash: Huayllacayán [3,626 m (?)[27]; 10°15′S, 77°26′W; also spelled Huayacayán], MUSM 2665. Provincia Bolognesi: Huanchay [1,857 m; 10°31′S, 77°25′W ; on the Quebrada Huanchay, a tributary of the Río Pativilca], MUSM 3025. Provincia Bolognesi, Distrito Huayllacayán: Yumpe [2,989 m; 10°15′S, 77°29′W], MUSM 3378, 3412–14, 3475. **Lima:** Distrito San Juan de Lurigancho: Canto Grande [311 m; 11°59′S, 77°01′W], MUSM 10034. Lomas de Atocongo [to 540 m; 12°08′S, 76°54′W], MUSM 19236. Lomas de Lachay [300–900 m; 11°21′S, 77°23′W], MUSM 2668 (paratype), 3400. Lomas de Lurín [10 m; 12°17′S, 76°52′W], MUSM 2171 (paratype). Radio Observatorio de Jicamarca [approximately 300–400 m; 11°57′S, 76°52′W], MUSM 2170 (holotype), 2173–74, 2867 (paratypes). Lomas de Pachacamac [75 m; 12°14′S, 76°53′W] (Carrillo de Espinoza, 1974). Provincia Huarochirí: Santa Eulalia [1,036 m; 11°51′S, 76°40′W], MUSM 3137.

[26] MCZ 17424 and 17427 were exchanged to the Instituto Butantan.

[27] According to the IGM 1:400,000 Ancash Department map, Huayllacayán is between 3,000 and 4,000 m. According to the Global Gazetteer, its elevation is 11,899 ft. (= 3,626 m), which is much higher than the next lower recorded elevation for *S. williamsi* (2,989 m). Another specimen, MUSM 3376, is listed from the same locality in the MUSM catalogues but explicitly notes the elevation as "2,700 m." The latter specimen is a juvenile with no discernible dorsal pattern, but all scutellation features are similar to *S. williamsi* except for 8 supralabials (4–5 touching the eye); in addition, the venter appeared to have large bold spots, which is uncharacteristic of most specimens of *S. williamsi*. For these reasons, I excluded MUSM 3376 from the study, but it indicates that specimens from this locality could come from lower elevations near Huayallcayán, in which case the upper elevational extent of *S. williamsi* is not known with precision. Another interpretation is that the catalogue entry "Huayllacayán" refers to the political unit district (Distrito) and not to the town of the same name.

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Anatomy of *Eocaecilia micropodia*, a Limbed Caecilian of the Early Jurassic

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ANATOMY OF *EOCAECILIA MICROPODIA*, A LIMBED CAECILIAN OF THE EARLY JURASSIC

FARISH A. JENKINS, JR.,[1] DENIS M. WALSH,[2] AND ROBERT L. CARROLL[3]

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ABSTRACT. *Eocaecilia micropodia*, an Early Jurassic caecilian from the Kayenta Formation of northeastern Arizona, is structurally comparable to Recent gymnophionans in numerous aspects but also possesses characters that are primitive or appear to be uniquely derived. The skull of *Eocaecilia* exhibits such distinctively caecilian features as (1) a sulcus along the orbital rim indicating the presence of a tentaculum; (2) an os basale representing consolidation of the supraoccipital, exoccipital, basisphenoid, basioccipital, pleurosphenoid, and parasphenoid elements; (3) an internal naris posterior to the premaxillary–maxillary suture and medial to the tooth rows on the vomer and palatine; (4) enlarged nasal capsules; and (5) an olfactory eminence on the vomer. As in Recent caecilians, the lower jaw comprises a pseudodentary and pseudoangular that are joined along an elongate, oblique suture. The pseudoangular bears a robust internal process and an elongate retroarticular process. The teeth are bicuspid and pedicellate, but are minute in size and are more numerous than in most living caecilians.

Several features of the skull and lower jaw of *Eocaecilia* are unexpectedly divergent from the pattern known in Recent gymnophionans. The apparent

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fusion of the stapes and quadrate is unique. The obliquely oriented, more or less planar jaw joint would appear to provide little stability, and is thus structurally and functionally unlike that known in any other caecilian. The internal process of the lower jaw is very robust, and projects into the adductor chamber.

Eocaecilia also presents primitive and/or transitional features that might be expected in forms representing an intermediate stage in the development of a specialized life style. The skull retains separate jugal, quadratojugal, postparietal, and ?tabular (or ?supratemporal) bones, elements that in living forms are either co-ossified with adjacent bones or lost. The limb girdles and limbs of *Eocaecilia* are a primitive retention, but the reduction in their relative size would appear to be transitional toward the limbless, gymnophionan condition.

Elongation of the body in *Eocaecilia* is estimated to be comparable to that in primitive extant gymnophionans, but a precise comparison cannot be made because of uncertainty over the number of vertebrae. In general, the postcranial axial skeleton is relatively primitive. Intercentra are present. The parapophyses are not protracted as elongate processes, as in living forms, nor is there a pronounced longitudinal keel on the ventral aspect of centra. In contrast to the atlases of Recent caecilians, an interglenoid tubercle is present. Processes projecting from the internal walls of the neural canal of the atlas and at least the next four postatlantal vertebrae represent attachment points for a suspensory ligament of the spinal cord. Such processes have not been previously reported in living caecilians but are now known to be present in representatives of various families (ichthyophiids, typhlonectids, and caeciliids). Neural spines are absent in the postatlantal and dorsal regions, as in living caecilians. Haemal arches are present in the tail, and distal caudal vertebrae bear posterodorsally recurved neural processes, as in rhinatrematids.

Although our knowledge of caecilian evolution and diversity now extends into the Early Jurassic, *Eocaecilia micropodia* does not provide sufficient evidence to securely recognize the origin of gymnophionans among known Paleozoic amphibians. The discovery of an operculum in *Eocaecilia micropodia* is novel confirmatory evidence that the opercular apparatus is a character shared with other lissamphibians. The absence of a separate operculum in extant gymnophionans may be hypothesized to relate to the loss of the shoulder girdle and the muscular link between the girdle and operculum. Nonetheless, a substantial morphological and temporal gap still intervenes in the identification of caecilian origins. Lissamphibia still remains at best a crown group concept, without a securely rooted stem in the Paleozoic.

INTRODUCTION

Fossil caecilians are sparsely represented in the geological record. Initially known only from an isolated vertebra from the Paleocene of Brazil (Estes and Wake, 1972), subsequent finds—vertebrae from the Paleocene of Bolivia (Rage, 1986) and the Cretaceous of Sudan (Evans et al., 1996; Werner, 1994) and the Miocene of Columbia (Hecht and Laduke, 1997)—offered scant evidence with which to probe the evolutionary history of the group. More recently, Evans and Sigogneau-Russell (2001) described the fragmentary remains of a primitive caecilian, *Rubricacaecilia monbaroni*, from the Lower Cretaceous of Morocco, adding further perspective on the Mesozoic record of caecilians. With fossil caecilians so rare, the discovery of *Eocaecilia micropodia* from the Early Jurassic Kayenta Formation of northeastern Arizona (Jenkins and Walsh, 1993) was particularly significant. This earliest known caecilian, abundantly represented by numerous cranial and postcranial specimens, possesses a number of features, including intercentra and limbs, which are primitive for the order but unknown in living representatives. Our descriptive account documents Early Mesozoic caecilian diversity in terms of characters that are clearly plesiomorphic, as well as features that are autapomorphic for gymnophionans.

In this study, we provide detailed documentation of the skull and postcranial skeleton of *Eocaecilia micropodia*, making anatomical comparisons with major features of Recent caecilians as well as with those few fossil forms that are known. We explore several specializations of *E. micropodia* in a functional context and finally consider the phylogenetic significance of this taxon in relation to current interpretations—and uncertainties—regarding the evolutionary history and relationships of caecilians.

The taxonomic terms "Apoda" and "apodans," used in reference to extant taxa as a group (cf. Trueb and Cloutier, 1991), is preoccupied (Dubois, 2004; Duellman and Trueb, 1986) and has been abandoned in this account. We follow the suggestion of Frost et al. (2006) that "Gymnophiona"

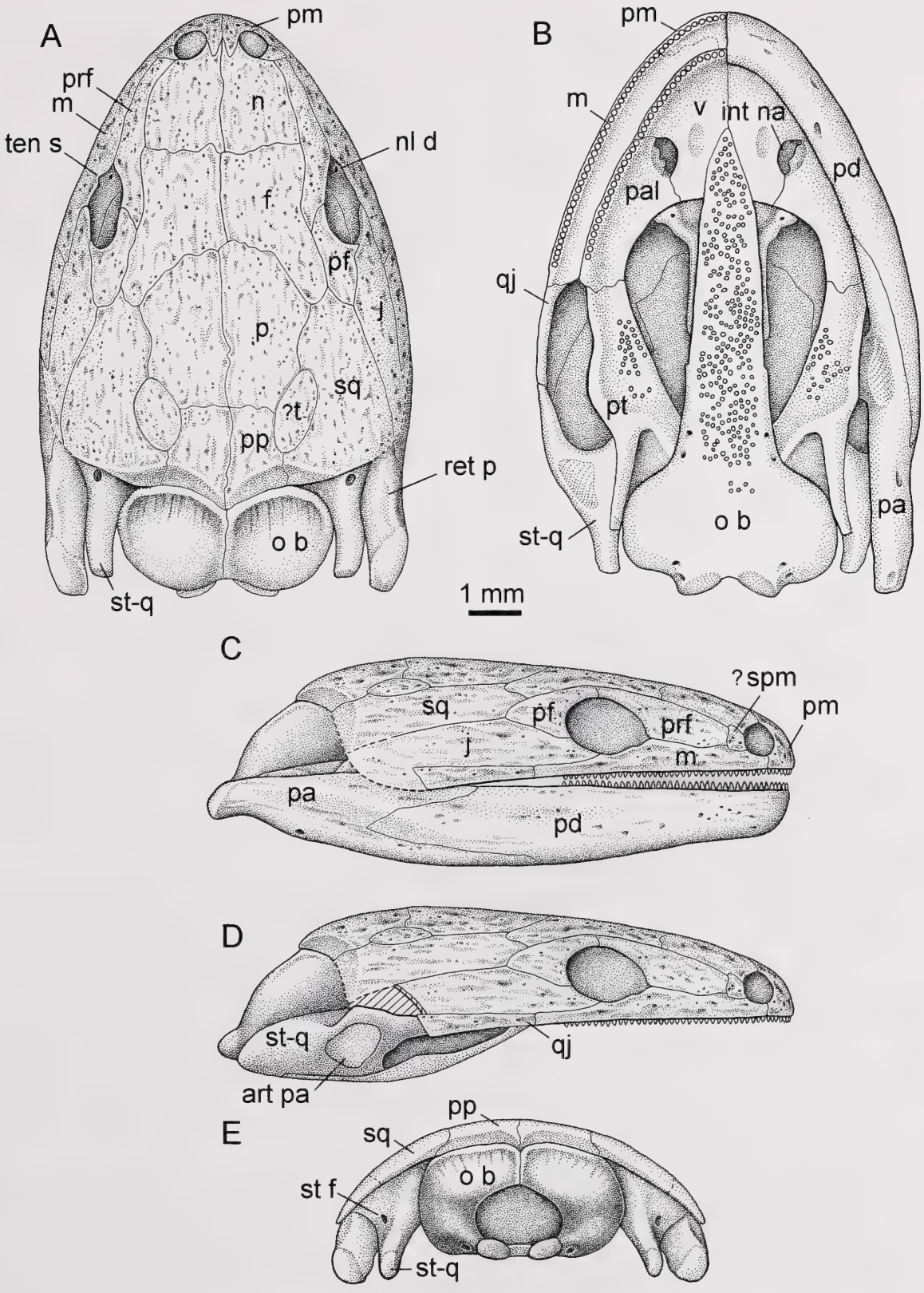


Figure 1. Reconstruction of the skull of *Eocaecilia micropodia* in (A) dorsal, (B) ventral, (C, D) lateral, and (E) occipital views. Major features, including size and general proportions, are based on the type (MNA V8066), but some details have been drawn from other specimens (MCZ 9169, 9015; MNA V8059, 8062). Postmortem compaction of the skulls renders the lateral and occipital views less reliable than the dorsal and ventral reconstructions. In D, the posterior end of the jugal (hatched area) has been truncated to reveal the dorsal margin of the stapes-quadrate.

be restricted to extant, limbless caecilians but do not adopt their proposed systematic reordering in face of incomplete results and ongoing analyses referred to in their work. We employ "caecilian" as an appropriate term for gymnophionans and their fossil relatives.

MATERIALS AND METHODS

Eocaecilia micropodia is represented by 40 specimens. Only two specimens are of more or less complete skulls with articulated lower jaws, but both have been subjected to postmortem compaction and fracturing. Nine specimens represent partial skulls (with or without lower jaws) in various stages of disarticulation, and six specimens are of isolated mandibles. Ten specimens are primarily postcranial: vertebrae, both in isolation and in short, articulated series; disarticulated appendicular elements; or both. The remainder of the collection consists of variably complete associations of cranial and postcranial bones. All of the material derives from a single locality, a quarry at Gold Spring (35°45′35″N, 111°04′51″W), approximately 300 m WSW of Gold Spring, Adeii Eechii Cliffs, Coconino County, Arizona, USA, in the silty facies of the Lower Jurassic Kayenta Formation. The Kayenta fauna, which also includes the anuran *Prosalirus bitis*, is probably at least Pleinsbachian in age if not slightly older (Shubin and Jenkins, 1995; Jenkins and Shubin, 1998). A complete list of the specimens is provided in the Appendix.

The jaw musculature of *Ichthyophis glutinosus* was studied by R.L.C. by frontal and sagittal serial sections and through dissections of preserved specimens prepared by David Dilkes. Bemis et al. (1983) discuss the diverse terminology of caecilian jaw muscles in the literature, reflecting perspectives that varied from morphological description to determination of homology. The present account follows the nomenclature of Lakjer (1926; also employed by Säve-Söderbergh, 1945), who based his identifications on the relationships of muscles to the branches of cranial nerve V, which are readily established in all living amphibian groups. Other descriptions of caecilian jaw muscles have commonly used the terminology of Edgeworth (1935), which differs significantly from that now broadly applied to all groups of terrestrial vertebrates, e.g., Carroll and Holmes (1980) for frogs and salamanders, Rieppel (1980) for squamates, and Bramble (1978) for mammals.

Institutional Abbreviations

FMNH	Field Museum of Natural History, Chicago, Illinois
LSUMZ	Louisiana State University Museum of Zoology, Baton Rouge, Louisiana
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
MNA	Museum of Northern Arizona, Flagstaff, Arizona

Abbreviations Used in Figures

Id	dorsal branch of the olfactory tract
Iv	ventral branch of the olfactory tract
II	optic nerve
V	trigeminal nerve
V_1	ophthalmic division of V
V_2	maxillary division of V
V_3	mandibular division of V
VII	facial nerve
AME	adductor mandibulae externus
AMI	adductor mandibulae internus
AMI(pr)	deep head of the adductor mandibulae internus (profundus)
AMI(su)	superficial head of the adductor mandibulae internus (superficialis)
AMP	adductor mandibulae posterior
AMP(lg)	adductor mandibulae posterior longus
art	articular facet
art pa	articular facet for pseudoangular
art pt	articular facet for pterygoid

art pt pal	articulation between pterygoid and palatine
art qu pt	articulating surface for quadrate ramus of pterygoid
art st-q	articular facet for stapes-quadrate
at	atlas
b cul pr	basin on the dorsal surface of the cultriform process
bp	basipterygoid process
c f	foramen for the carotid artery
cor f	coracoid foramen
cul pr	cultriform process
DM	depressor mandibulae
ect	ectopterygoid
ex n	external naris
f	frontal
fb	fibula
fe	femur
f im	intramandibular foramen
f o	fenestra ovalis
g pt m	groove for pterygoideus muscle
gl	glenoid
gr art sph	groove for articulation with the sphenethmoid
gr pt m	groove for pterygoideus muscle
h	humerus
h a	haemal arch
ic	intercentrum
IH	interhyoideus
IHP	interhyoideus posterior
IM	intermandibularis
int na	internal naris
int p	internal process
j	jugal
j f	jugular foramen
lat tr	lateral (labial) tooth row
LQ	levator quadrati
m	maxilla
med t r	medial (lingual) tooth row
m f	mandibular (adductor) fossa
mp	maxillopalatine
mta	metatarsal
n	nasal
nl d	nasolacrimal duct
o b	os basale
o c	otic capsule
o con	occipital condyle
op	operculum
o r	otic ridge for contact with skull roof
orb	orbit
p	parietal
pa	pseudoangular
pal	palatine
p con	processus conchoides
pd	pseudodentary
?pel	possible pelvic element
pf	postfrontal
ph	phalanges
p i p	internal process of pedicle
pl	pleurosphenoid
pm	premaxilla
pp	postparietal
pr	parietal ridge
prf	prefrontal
pt	pterygoid
PT	pterygoideus muscle
q	quadrate
qj	quadratojugal
q r pt	quadrate ramus of the pterygoid
r	rib
rad	radius
ret p	retroarticular process
sc	scapulocoracoid
sph	sphenethmoid
spm	septomaxilla
?spm	possible septomaxilla
sq	squamosal
st	stapes
st f	stapedial foramen
st-q	stapes-quadrate
?t	?tabular
tb	tibia
ten	tentacle
ten o	tentacular opening
ten s	tentacular sulcus
u	ulna
v	vomer
ver	vertebra
ver cd	caudal vertebra(e)
ver d	doral vertebra(e)
ver patl	postatlantal vertebra
v f	vascular foramen
v s	vomerine sulcus

DESCRIPTION

Skull

The skull of *Eocaecilia micropodia* was recognized by Jenkins and Walsh (1993) as sharing a suite of features that are distinctively caecilian, including a well ossified, compact skull roof, a tentacular sulcus, and a large retroarticular process on the lower jaw. The skull appears to have been relatively low, as in most modern caecilians, but all specimens have been dorsoventrally crushed to a variable degree. In dorsal view (Fig. 1A), the most conspicuous feature is the extension of the braincase behind the posterior margin of the skull roof; as a consequence, the jaw articulation is situated in a relatively anterior position (Fig. 1D). The orbits are large compared with those in most Recent caecilians but are small relative to those in Paleozoic tetrapods of similar body size (e.g., gymnarthrids, goniorhynchids, and amphibamids). The mouth, which Jenkins and Walsh (1993) reconstructed as only slightly subterminal, is here reconstructed with essentially no premaxillary overhang, in contrast to the subterminal condition typical of gymnophionans. The skull table and cheek are a continuous bony shield, as in some Recent caecilians.

Evidence of variation in skull size is modest. The length and width of the type (MNA V8066, Figs. 2–4), which is the most complete and least distorted specimen, are 12.7 and 8 mm, respectively. Length was determined in the midline from the tip of the rostrum to a line transversely tangential to the occipital condyles and is equivalent to Lessa and Wake's (1992) measurement 5 in their morphometric study of *Dermophis mexicanus*. Width was determined from the most broadly separated points on the sides of the skull; this measurement approximates but is not exactly equivalent to "skull width at jaw articulation," measurement 3 of Lessa and Wake (1992, appendix 1; incorrectly labeled as "40" on fig. 1). Estimates of other skull lengths and widths are 13.5 and 8.2 mm (MCZ 9169, Fig. 5) and 9.8 and 7.2 mm (MCZ 9015), respectively. The skull of MNA V9346 (Fig. 11) is 14 mm in length but does not permit a reliable measure of width. MNA V8062 (Fig. 8) is too incomplete to provide a direct linear estimate of length, but on the basis of the dimensions of the frontal bone, the skull would appear to have been comparable in size to that of the holotype.

No single specimen shows all elements, but nearly all of the dermal skull can be reconstructed by comparing and compiling structural data from the following specimens: the type specimen, MNA V8066 (Figs. 2–4), a nearly complete skull prepared in dorsal and ventral views; MCZ 9169 (Fig. 5), most of a skull exposed in dorsal view; MCZ 9015 (Fig. 13A, B), a nearly complete skull exposed in dorsal and ventral aspects; MNA V8059 (Fig. 7), exhibiting palate, jaws, both stapes-quadrates, and the underside of the skull roof; MNA V8062 (Fig. 8), a right antorbital region; and MNA V9346 (Fig. 11, a palate and lower jaws in ventral view.

Further study of the material since Jenkins and Walsh's (1993) initial description has resulted in some modifications to the previously interpreted pattern of dermal bones. In some cases, a coating of Glyptal applied to the external surface of the skull roof illuminated narrow, pigmented bands on either side of barely visible sutures. The new findings are the presence of distinct postparietals and ?tabulars/?supratemporals; concrete evidence for the presence of both a postorbital and a postfrontal in the circumorbital series is lacking.

Skull Roof. Almost all of the bones that ancestrally compose the amphibian skull roof are present. In contrast to all Recent caecilians, the skull in *Eocaecilia micropodia* retains the postparietal, jugal, quadratojugal, and ?tabular/?supratemporal; the last three are evident in the type. The sculpturing of the bones indicates that the dermis was firmly adherent to the skull roof, as in Recent taxa.

Postparietals are not readily apparent in

the type specimen and were not recognized as distinct elements by Jenkins and Walsh (1993). However, separate postparietals are evident in MCZ 9169 (Fig. 5), in which they are suturally delineated from surrounding bones. Once observed in this specimen, the presence of postparietals in the holotype was detected through an application of the Glyptal technique described above, which revealed the sutural lines separating parietals from postparietals. Similar bands became evident along both sides of the sutures separating parietals and frontals and at the anterior margin of the frontal in the type, but not in other specimens, in which the bones are more coarsely sculptured. In most modern caecilians (e.g., in *Ichthyophis glutinosus,* Fig. 6A), the parietals are longer than the frontals, as would be expected if they incorporated the area that was originally formed by the postparietals. The postparietals exhibit a slightly recessed area of smooth bone surface posteriorly, which was presumably covered by an anterior extension of the dorsal trunk musculature, as is the case in living caecilians.

An irregular, inconsistently shaped bone lies in the position of a tabular or supratemporal in Paleozoic tetrapods. This element, which we tentatively interpret as a ?tabular (Figs. 1, 2, 5, 7), appears to have been relatively loosely articulated with adjacent dermal bones, overlying ventral lappets of the surrounding bones without being suturally interdigitated. In the type (Fig. 2), the right tabular is close to a normal position, but the left has slipped over the left side of the os basale. The left tabular is also displaced posteriorly in MCZ 9169 (Fig. 5). The posterior margin of the tabular is not complete in any specimen, obviating the possibility of determining whether this bone reached the posterior margin of the skull, as is the case in most Paleozoic tetrapods.

The large squamosal, best preserved in MNA V8059 (Fig. 7), forms much of the cheek region. The great width of the squamosal suggests that it probably reached the postparietal, posterior to the tabular. The smooth, thickened medial margin would appear to have abutted the parietal and tabular by a squamous suture in which the adjacent bony margins are reciprocally beveled (rather than by serrate interdigitation). The articular relationship between the squamosal and dermal skull roof in *Eocaecilia micropodia* thus is comparable to that in many stegokrotaphic gymnophionans in which the squamosal is attached to the skull roof by a sutural ligament; the ligament in some taxa is so broad that an apparent "gap" appears on dried skulls. In none of the specimens of *E. micropodia* is the posterolateral portion of the squamosal sufficiently well preserved in dorsal view to determine the configuration of the occipital margin or show the area from which the depressor mandibulae originates in Recent caecilians. The anterior extremity of the squamosal narrows to an acute terminus between the frontal and postfrontal.

In *Eocaecilia micropodia,* the ventral part of the cheek is formed by a large jugal, which extends rostrad to form the posteroventral margin of the orbit, and a long, slender quadratojugal (Figs. 1C, D, 2). In Recent caecilians, a separate quadratojugal is not known to be retained in the adults of any species; thus, the squamosal extends to the inferior margin of the skull. Peter (1898) proposed that the quadratojugal of *Ichthyophis glutinosus* has been incorporated into the quadrate as an anteriorly projecting, laminar process, an interpretation that was adopted by de Villiers (1936) and Visser (1963). In a developmental study of two species of *Epicrionops,* Reiss (1996) identified the "quadratojugal process" as a feature appearing late in ontogeny but presented no evidence for its derivation from a quadratojugal. Studies of *Dermophis mexicanus* by Wake and Hanken (1982) and *Gegeneophis ramaswamii* by Müller et al. (2005) concluded that the quadratojugal is absent. The interpretation of Marcus et al. (1935: 411) that a quadratojugal ("quadratomaxillare") anlagen is

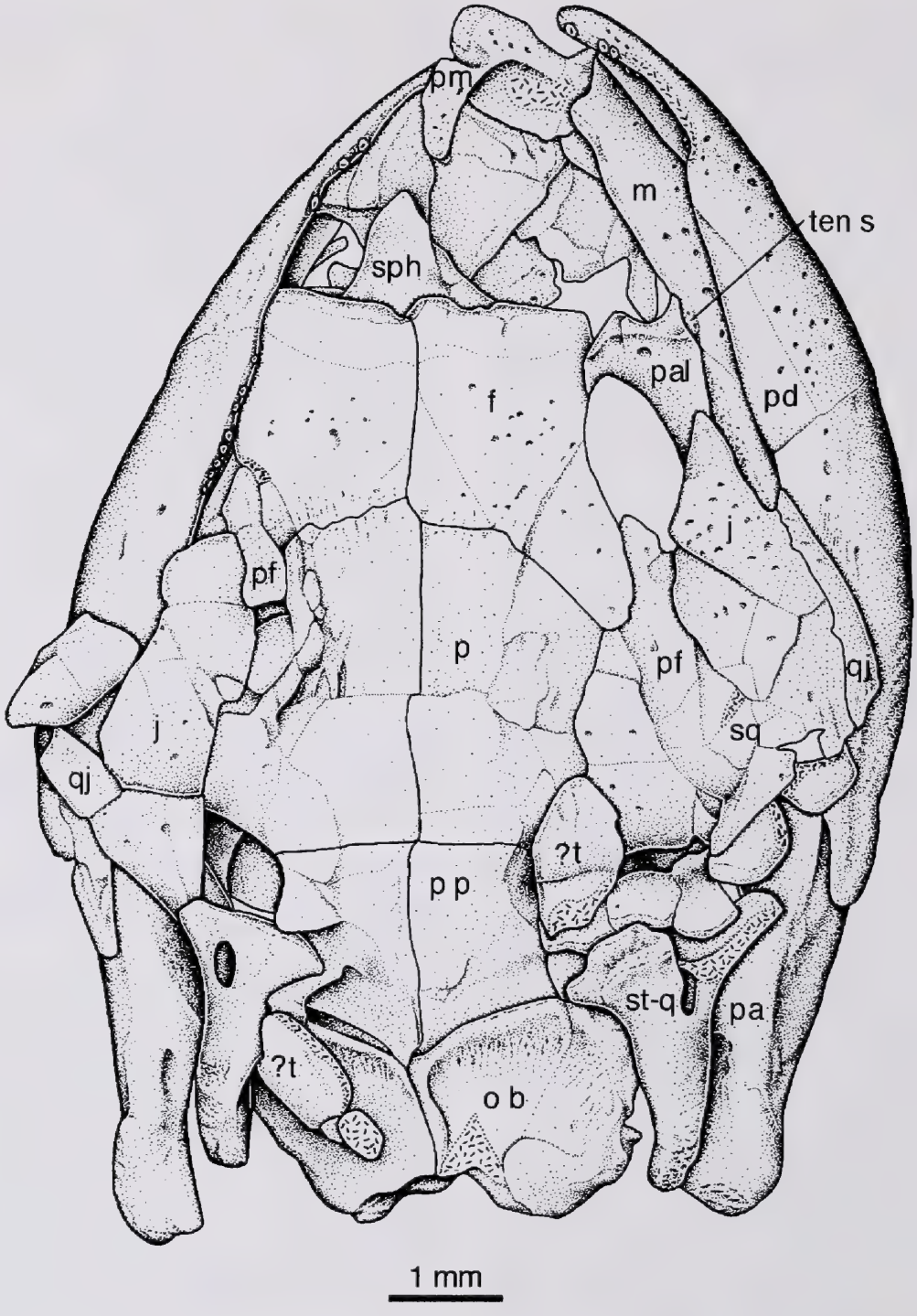


Figure 2. Skull of the type specimen of *Eocaecilia micropodia* (MNA V8066) in dorsal view.

present during development is rendered moot by the observations of Wake and Hanken (1982: 211), who noted several sources of possible error, in addition to the inclusion of different genera in a "single" growth series. Thus, at best, the evidence for the retention of a quadratojugal vestige in living caecilians is equivocal; yet, there is no doubt that a distinct quadratojugal persisted as the posterolateral marginal element of the dermal skull roof until at least the Jurassic.

The large, rectangular nasal, most clearly preserved on the left side of MCZ 9169 (Fig. 5), is incised rostrally at the premaxillary articulation. The nasals are missing

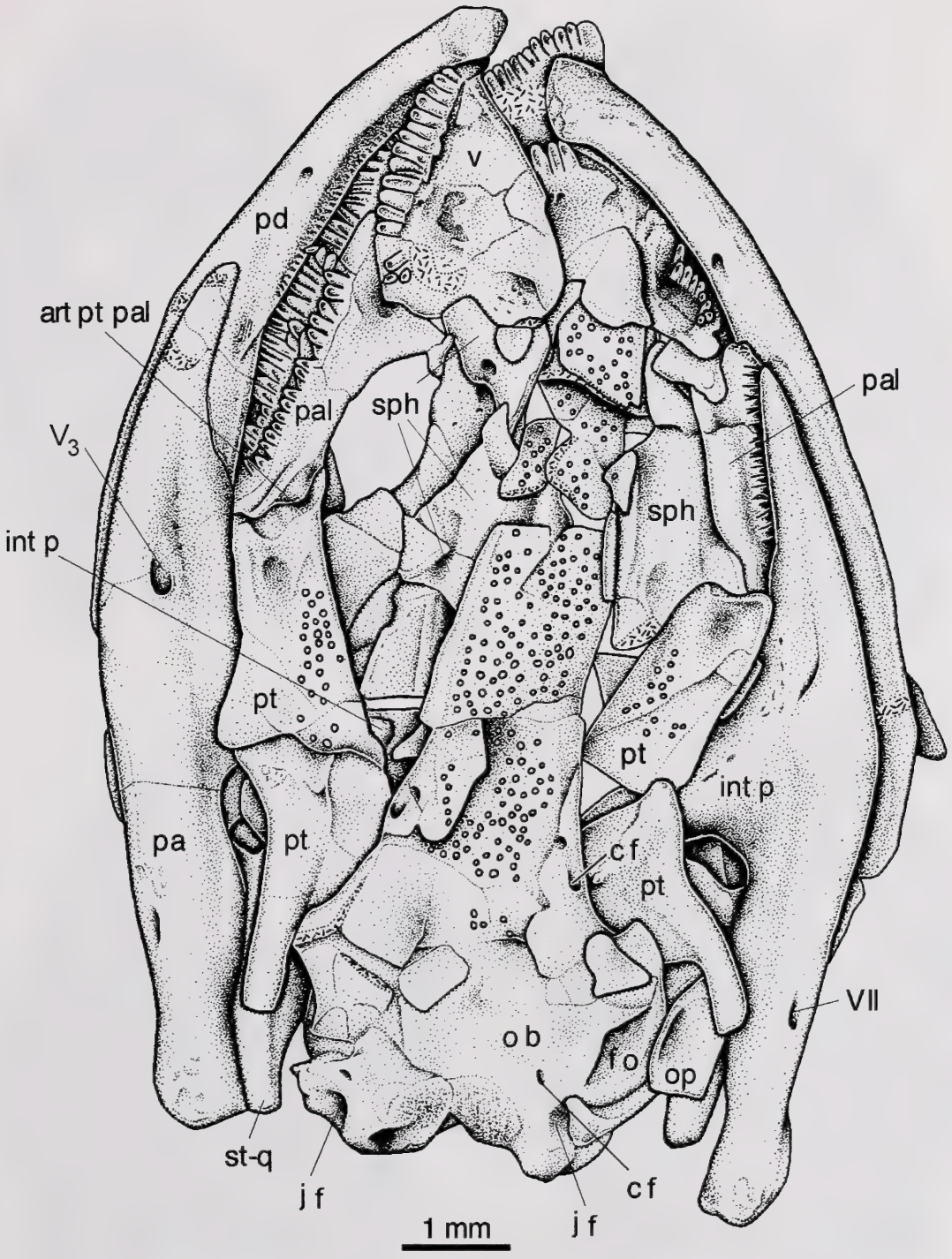


Figure 3. Skull of the type specimen of *Eocaecilia micropodia* (MNA V8066) in ventral view. Both pterygoids (pt) have been broken transversely by postmortem crushing against the adjacent internal process (int p) of the pseudoangular; in life, each internal process projected into the adductor chamber above the level of the pterygoids.

in the type (Fig. 2) and on the right side of MCZ 9169 (Fig. 5), suggestive evidence that they might have been only loosely attached to the frontals.

The long, rectangular prefrontal, best preserved in MNA V8062 (Fig. 8), extends from the midpoint of the dorsal orbital rim to the narial margin. A prefrontal is present in the Ichthyophiidae, Uraeotyphlidae, and Scolecomorphidae, but the bone has been lost or become incorporated into the maxillopalatine in other taxa (Nussbaum and Wilkinson, 1989).

The configuration of the posterior or-

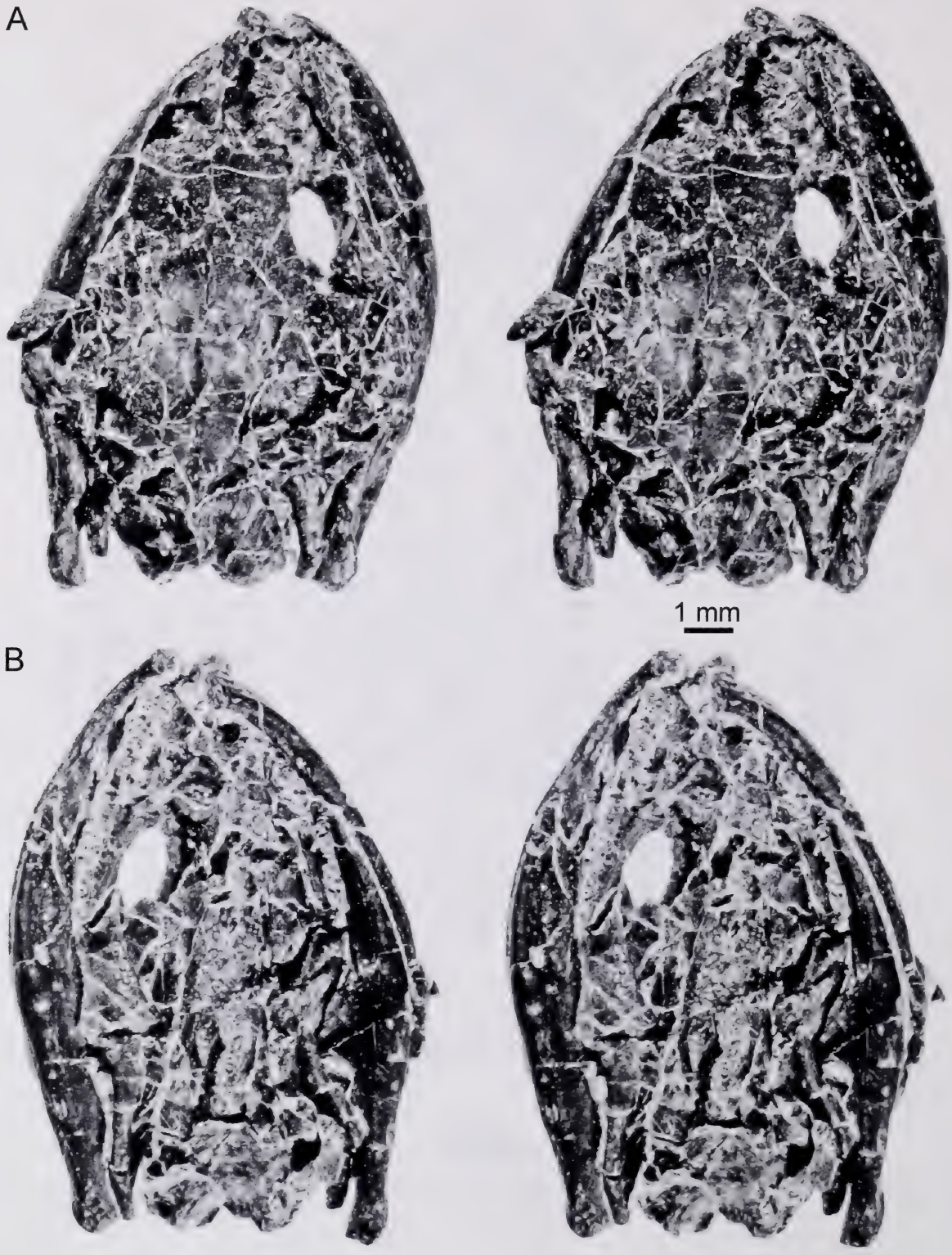


Figure 4. The skull of the type specimen of *Eocaecilia micropodia* (MNA V8066) in (A) dorsal and (B) ventral views (stereophotographs).

bital margin in *Eocaecilia micropodia* is somewhat equivocal because all specimens are to some degree damaged in this area. In most Paleozoic tetrapods two bones—a postfrontal and a postorbital—contribute to the posterior orbital margin. Jenkins and Walsh's reconstruction (1993, fig. 2b) of *E. micropodia* depicted both bones, an interpretation based primarily on the right side of the holotype (Fig. 2) where there

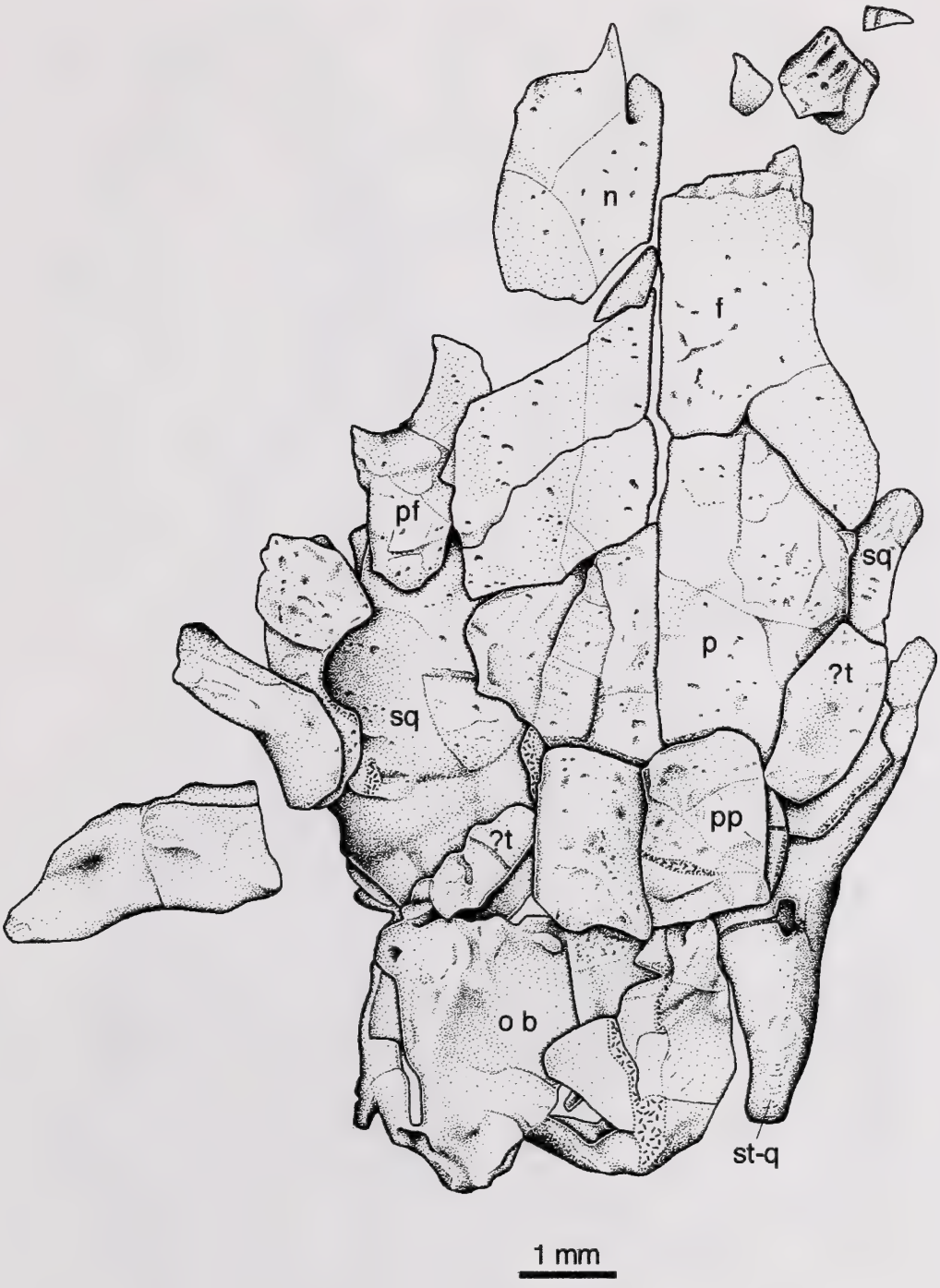


Figure 5. *Eocaecilia micropodia,* dorsal view of the skull of MCZ 9169. Left stapes-quadrate has been removed (see Fig. 20). On the right side, the stapes-quadrate is intact and nearly in its natural position, exposing much of the dorsal and lateral surface. The posterior portion of the bone was removed from the left side so that it can be viewed in all aspects, but the anterior extremity was not complete.

appears to be two elements. Both have been displaced ventrally by crushing, and the adjoining margins are sufficiently obscured that it is not possible to determine definitively whether there are two bones separated suturally or a single element fractured longitudinally. Several other skulls, however, provide evidence that favors the latter interpretation. The left side of MCZ 9169 (Fig. 5) shows only a single bone composing the posterodorsal margin of the orbit. Similarly, but a single element forms the posterodorsal orbital margin in MNA V8059 (Fig. 7); on the left side are

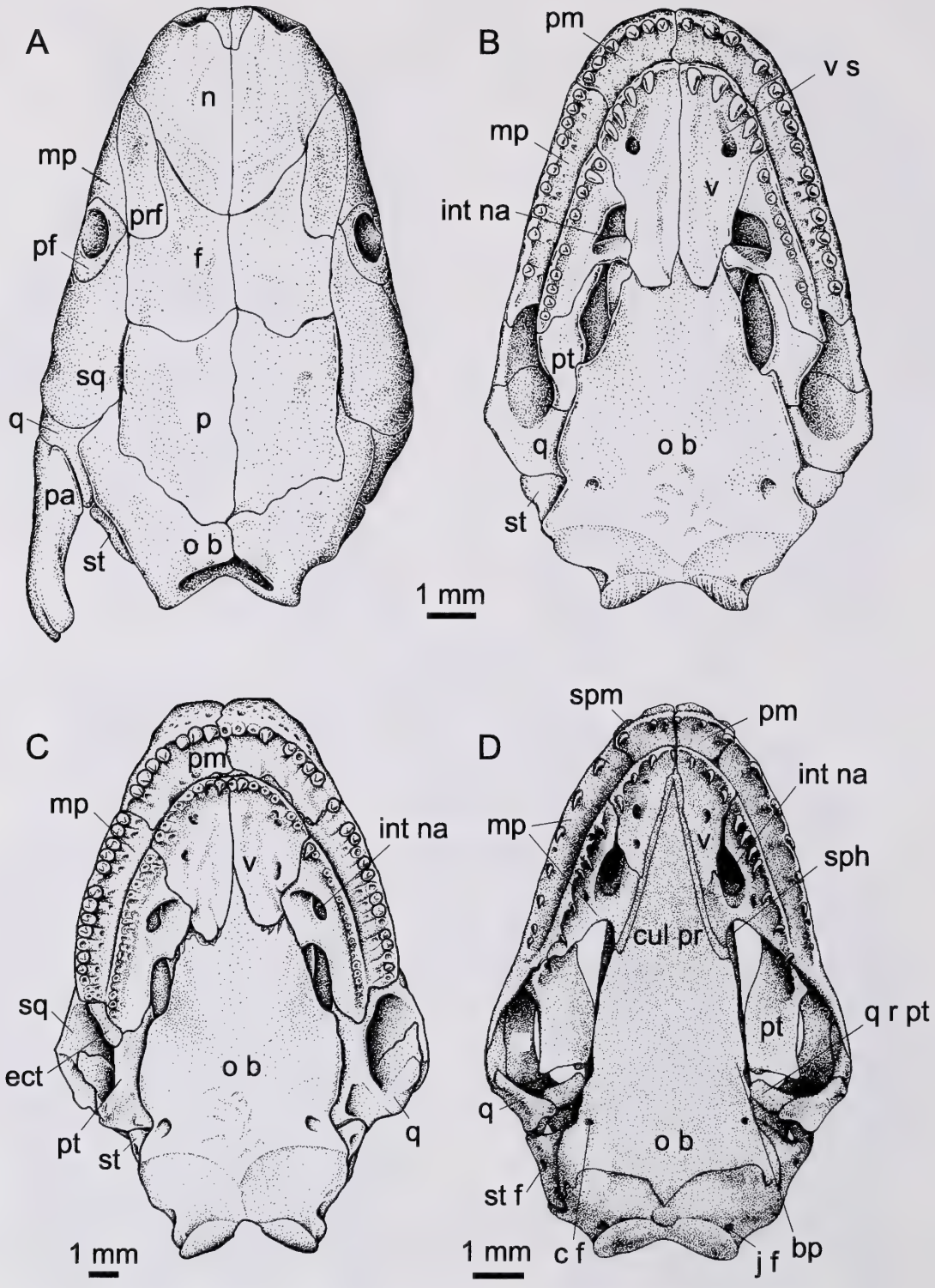


Figure 6. Skull roof and palate of gymnophionans. (A) Skull roof of *Ichthyophis glutinosis*. (B) Palate of *Ichthyophis glutinosis*. (C) Palate of *Gymnopis multiplicata* (FMNH 189131). (D) Palate of *Epicrionops petersi*. Plates A and B drawn are rendered from photographs in Taylor, 1969; plate D is reproduced from Nussbaum (1977, fig. 1).

part of the jugal and a maxillary fragment, and on the right, a sutural contact with the prefrontal is preserved. Cognizant of the limited evidence and the lack of a complete orbital margin, we nonetheless favor the interpretation that *E. micropodia* possessed only a single postfrontal/postorbital element. No living caecilian possesses two elements in this region. Representatives of only two families (Ichthyophiidae, Uraeo-

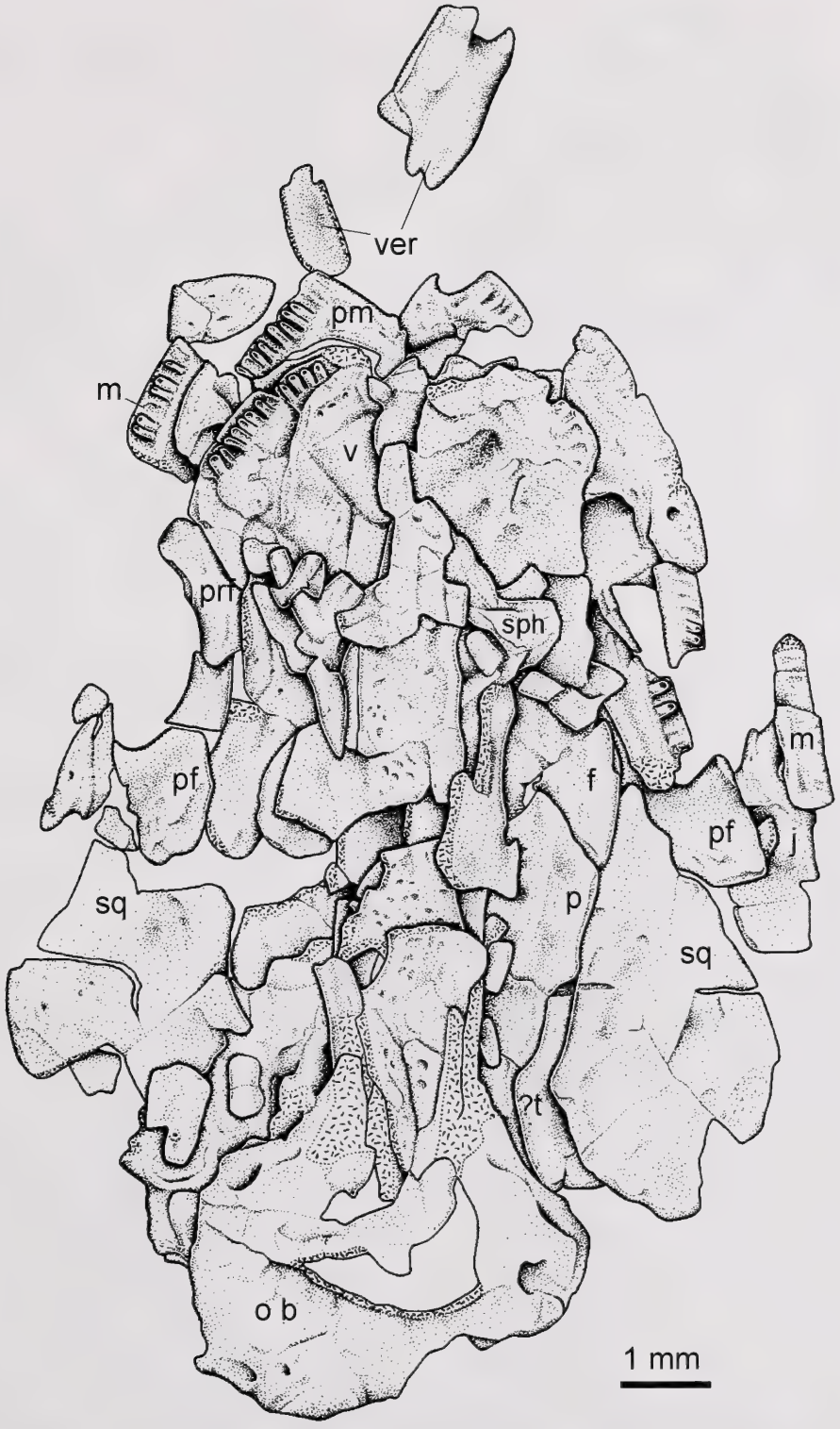


Figure 7. *Eocaecilia micropodia,* MNA V8059, ventral view of the skull roof and palate.

typhlidae) possess a putative postfrontal, which could be distinct or partially or entirely fused to the maxillopalatine (Nussbaum and Wilkinson, 1989). The "postfrontal" of living caecilians is thus a conventional designation for the single ossification that nearly encircles the eye (cf. *Ichthyophis glutinosus,* Fig. 6A; *Uraeotyphlus narayani,* Nussbaum, 1979, fig. 1), occupying the circumorbital margin that in *E. micropodia* is formed by the prefrontal, postfrontal, and jugal bones.

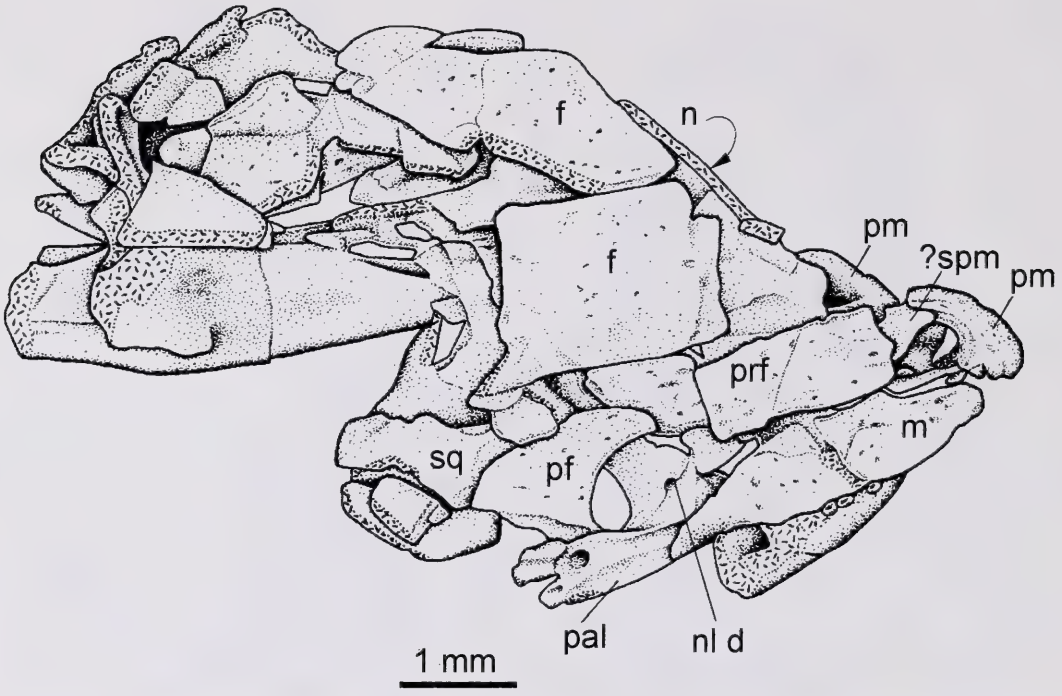


Figure 8. *Eocaecilia micropodia,* MNA V8062, dorsolateral view of a partial skull of which only the anterior part is preserved.

The lacrimal bone presents the most equivocal case for interpretation of any of the skull roof elements. In the only specimen for which the lateral surface of the antorbital region is articulated (MNA V8062, Fig. 8), there appears to be a narrow triangular space between the posterior portion of the prefrontal and maxilla that might have been occupied by a lacrimal. Although a lacrimal is not known in the adult of any Recent caecilian, a separate element in the nasal region of embryonic *Ichthyophis glutinosus* was identified by Peter (1898, fig. 20) as a turbinale (= lacrimal). Similarly, Marcus et al. (1935, fig. 5) identified a lacrimal in their reconstruction of a 68-mm embryo of *Grandisonia alterans* (cf. Wake and Hanken, 1982, table 1). Wake and Hanken (1982), however, found no evidence of a separate lacrimal ossification center in their study of *Dermophis mexicanus*; in view of their cautionary assessment of the evidence presented by Marcus et al. (1935) for multiple ossification centers (including that for the quadratojugal, postparietal, periorbital, ectopterygoid, and interparietal), the fate of the lacrimal in caecilian history must be regarded as unresolved.

The premaxilla, which does not appear to overhang the lower jaw as it does in many Recent caecilians, has a long posterodorsal process that fits into a slot in the nasal and a very narrow extension that occupies a groove along the anterodorsal margin of the maxilla. As is the case for almost all specimens of upper and lower jaws, the crowns of the teeth have disarticulated postmortem from the pedicels; only in the premaxilla of MNA V9346 do a few crowns appear to be preserved in situ. The premaxilla in MNA V8059 (Fig. 7) bears approximately 10–12 tooth positions (10 as actual pedicels and 2 as spaces wide enough to accommodate a pedicel). The pedicels are formed as elongate, narrow tubes that are fused to the inside of the jaw margin. The diameter of premaxillary pedicels was measured with an optical micrometer on specimens in which individual pedicels are well preserved. Four pedicels on MNA V8059 have diameters of 0.10, 0.12, 0.13, and 0.13 mm. One premaxillary pedicel on MNA V9346

has a diameter of 0.14 mm, and an adjacent (disarticulated) tooth crown measures 0.12 mm in basal diameter and 0.22 mm in apicobasal height.

Our present interpretation of the septomaxilla in *Eocaecilia micropodia* differs from that originally proposed (Jenkins and Walsh, 1993, fig. 2b) and is based on a displaced bone in a single specimen (Fig. 8). The bone might have contributed to the posterior margin of the narial opening, as in the case in some extant caecilians. A septomaxilla is present in ichthyophiids, rhinatrematids, uraeotyphlids, and scolecomorphids but is absent as a separate element in typhlonectids and caeciliids (Nussbaum, 1977, 1979; Taylor, 1969; Wake, 2003).

The maxilla is a long, narrow bone that contributes to the anteroventral margin of the orbit for a short distance. The most completely preserved maxilla is on the right side of the type (Fig. 2), but the inferior margin and maxillary teeth are obscured by the overlying, displaced lower jaw. No specimen shows the entire maxillary tooth row. The number of maxillary teeth is probably in the range of 32–39, an estimate based on the length of the maxilla in the type (4.9 mm) and the number of pedicels per millimeter on maxillary fragments of other specimens. Pedicels per millimeter varied from 6.5 on a left anterior maxillary fragment of MNA V9346 to 8 in a right anterior maxillary fragment of MNA V8059 (seven well-preserved maxillary pedicels on the latter specimen range from 0.1 to 0.13 mm in diameter, with a mean of 0.11 mm). Intermediate values of 7.5 were measured from other maxillary fragments (MCZ 1956, MNA V8059, and MNA V8062).

In contrast to Recent caecilians, the maxilla is not fused to the palatine; a suture delineating the adjacent borders of these bones is clearly preserved in MNA V8062 (Fig. 8). The margin of the maxilla that borders the anteroventral rim of the orbit is incised by a shallow, broad sulcus in both the type of *Eocaecilia micropodia* (Fig. 2) and in MCZ 9156 (Figs. 9, 10C). The sulcus is confluent with a comparably smooth depression in the adjacent palatine. We interpret this feature as marking the course of the tentacle as originally proposed by Jenkins and Walsh (1993). Early ontogenetic development of the tentacle in *Dermophis mexicanus* is in close association with the eye, from which various components of the tentacular apparatus are coopted (e.g., the Harderian gland, extraocular muscles and nerves, and lacrimal ducts, among others; Billo and Wake, 1987; Wake, 1992). Although the tentacle in most living caecilians passes through an aperture that is separate from the orbit (Fig. 10A), in rhinatrematids the tentacular opening is not separate (Fig. 10B) but is merely "a small longitudinal slit" along the anterior margin of the orbit (Nussbaum, 1977: 7). In fossil caecilian material, the presence of a tentacular apparatus could only be inferred with certainty if a separate tentacular foramen were present, but the slight depression of the orbital margin in *E. micropodia* (Fig. 10C) is at least consistent with the expected primitive position of this organ.

Sculpturing of the Skull Roof. Most cranial specimens of *Eocaecilia micropodia* possess a shallow rugosity on the superficial surface of the dermal bones comparable to that developed in some larger, extant caecilians (e.g., *Gymnopis* spp.). The skull of the type specimen also exhibits small, scattered foramina (Fig. 2). These foramina, which distribute nerves and nutrient vessels, are most numerous on the bones surrounding the orbit and adjacent to the jaw margins, as in living species (Taylor, 1969), but also occur sporadically on the bones that border the midline of the skull roof.

Palate. The palate of *Eocaecilia micropodia* demonstrates that basic features retained among extant caecilians were acquired by the Jurassic, in contrast to the pattern of dermal bones of the skull, which is only modestly altered from that common among Paleozoic amphibians. A principal

feature is a continuous row of teeth that spans each vomer and palatine, paralleling the row on the premaxilla and maxilla (Figs. 1B, 3, 7). The most complete series of pedicels is preserved on the right side of the type (MNA V8066, Fig. 3) where the vomer and palatine each bear approximately 17 teeth. In this series, nine well-preserved palatal pedicels selected for measurement range in diameter from 0.1 to 0.14 mm (mean 0.12 mm) and are comparable in size to those on the maxilla and premaxilla measured from other specimens. On MNA V8059, five pedicels that could be measured range from 0.11 to 0.15 mm in diameter (mean 0.13 mm). A series of 13 pedicels on the vomer of MCZ 9242 (Fig. 12) is the most perfectly preserved palatal row available with which to assess detailed geometry. All the pedicels are slightly oval in cross section, with the labiolingual axis slightly longer than the mesiodistal axis. Labiolingual axes range from 0.14 to 0.18 mm (mean 0.17 mm), whereas mesiodistal axes range from 0.12 to 0.14 mm (mean 0.135 mm). The height of the pedicels ranges from 0.35 to 0.37 mm. Lingual to and between the 11th and 12th pedicel in this series is an inverted tooth crown (circular in cross section, with a diameter of 0.1 mm).

The distance between the premaxillary–maxillary and vomerine–palatine tooth rows varies among extant caecilians, being relatively narrowly separated in species of *Ichthyophis* and well separated in species of *Caecilia* (Taylor, 1969). Direct assessment of this feature in *E. micropodia* is precluded by the fact that, in all specimens with an intact palate, the lower jaws remain in position, concealing the most lateral part of the palate and the premaxillary–maxillary tooth row. However, in view of the close juxtaposition of the tooth rows of the lower jaw, the separation of the palatal and marginal rows was probably only slightly greater (for further analysis, see *Lower jaw*).

The vomers meet anteriorly along a median suture for about half their length. Posteriorly, the medial margins of the vomers are separated by the relatively broad rostral end of the cultriform process of the parasphenoid component of the os basale, which intervenes to complete the bony palate in this area (Fig. 1B). The degree to which the cultriform process is exposed between the recessed medial margins of the vomers in *Eocaecilia micropodia* would appear to be intermediate between the extremes observed in extant caecilians (cf. Trueb, 1993: 275, table 1; Wake, 2003). In the rhinatrematid *Epicrionops petersi* (Fig. 6D), the vomers meet rostrally only along a very short suture; the cultriform process is extensively exposed between them. In ichthyophiids (Fig. 6B) and many other caecilians, by contrast, the vomers are united for nearly their entire length along the median suture. Intraspecific variations can also be substantial, as in *Gymnopis*; in *G. multiplicata* (Taylor, 1969, fig. 34), the vomers are separated for almost their entire length, whereas in *G. multiplicata proxima* (Fig. 6C; see also Taylor, 1969, fig. 35), the vomers are united for more than half their length.

In most Recent caecilians, the vomer is pierced by a large foramen (in some cases two) anteromedial to the internal naris (Taylor, 1969). In *Ichthyophis glutinosus* (Fig. 6B), this opening provides passage for the palatine branch of the facial nerve (VII) and a vein from the snout and dorsal surface of the palate; a rostrocaudally aligned neurovascular sulcus leads to the foramen's palatal opening. In *I. glutinosus*, the vomerine foramen and sulcus on the palatal surface correspond in position to a ridge on the dorsal surface of the vomer; this ridge, the olfactory eminence (Fig. 14A), divides the large nasal sacs into medial and lateral cavities (Badenhorst, 1978, fig. 9; Schmidt and Wake, 1990). Although there are no large vomerine foramina in *Eocaecilia micropodia*, numerous small foramina are variably developed on the bone's palatal surface. A consistent feature is a sulcus on the palatal surface of the vomer, anteromedial to the internal naris.

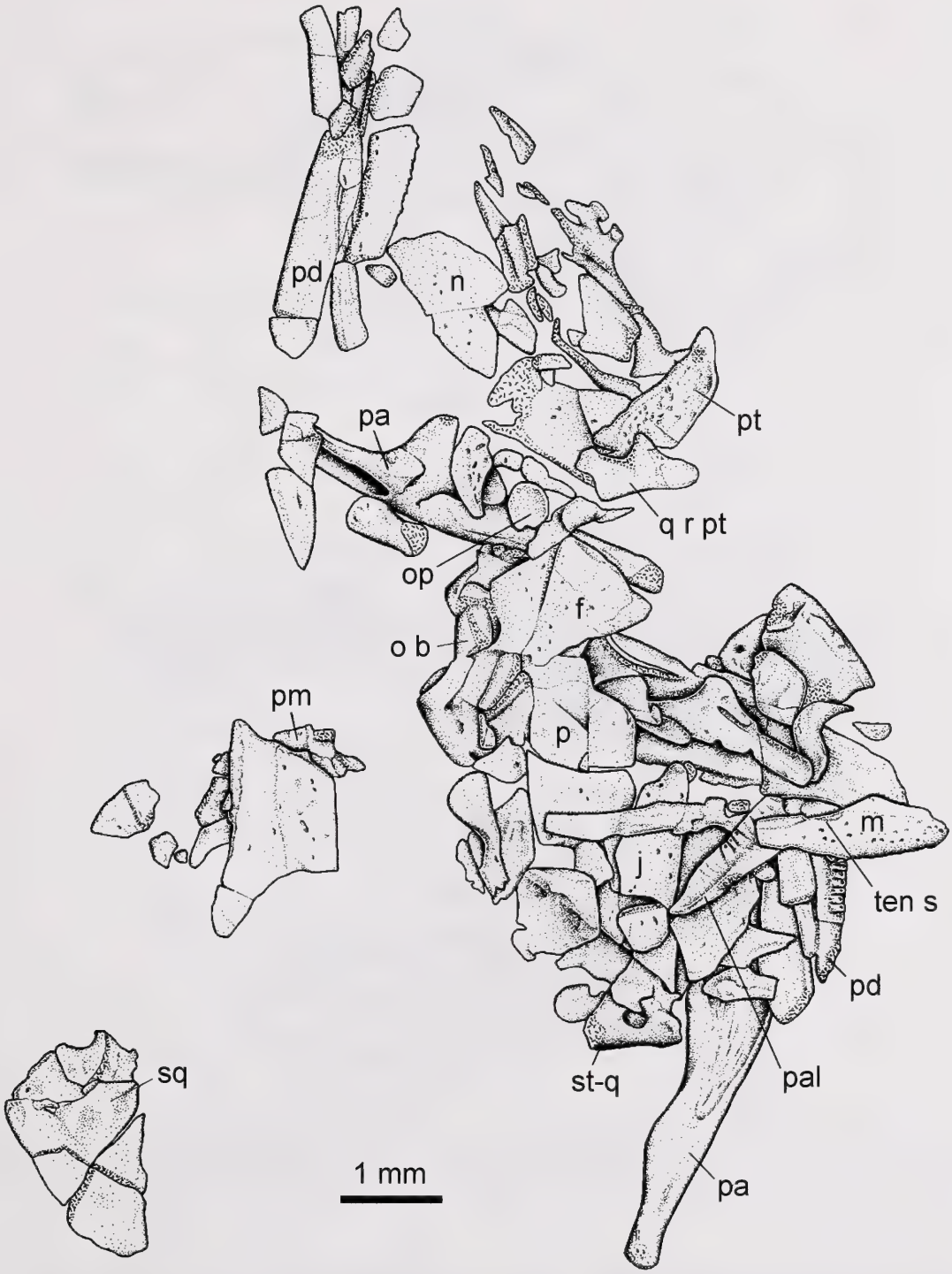


Figure 9. *Eocaecilia micropodia,* MCZ 9156, the disarticulated elements of a skull. For details of the maxilla (m) and tentacular sulcus (ten s), see Figure 10C.

The depression is evident on both vomers of MNA V9346 (v s, Fig. 11) and on the single vomer present in MCZ 9242 (Fig. 12). The corresponding elevation of the dorsal surface of the vomer might possibly represent an olfactory eminence (cf. Fig. 14A).

The internal nares of *Eocaecilia micropodia* open medial to the internal row of teeth, rather than adjacent to the suture between the maxilla and premaxilla as in most Paleozoic tetrapods. Both the vomer and palatine contribute to the margin of the internal naris, a condition that is com-

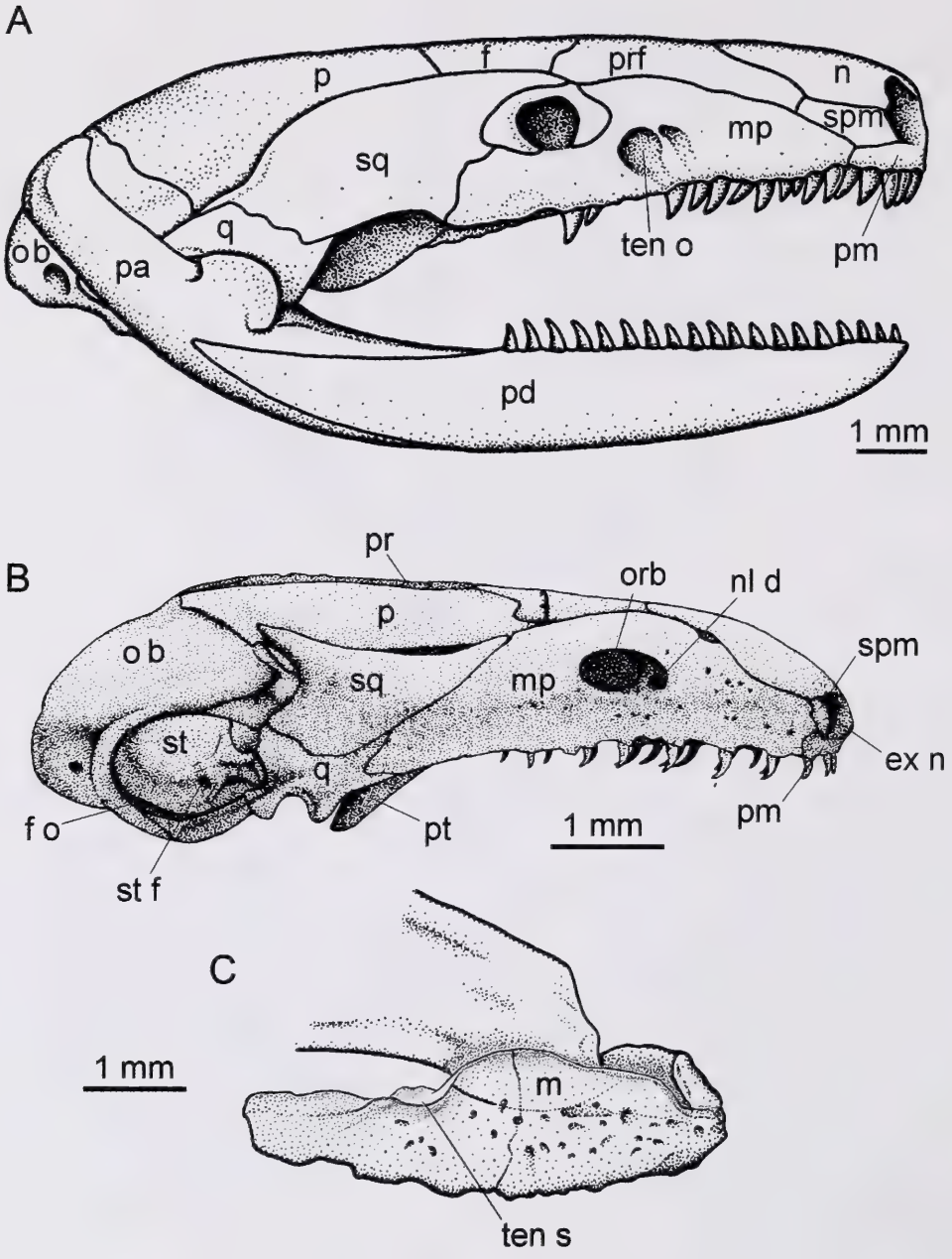


Figure 10. (A) A skull and lower jaw of *Ichthyophis glutinosus* (skull drawn from Taylor, 1969, fig. 2; lower jaw drawn from Sarasin and Sarasin, 1887–1890, pl. 15, fig. 3). (B) Lateral view of the skull of *Epicrionops petersi* (reproduced from Nussbaum, 1977, fig. 1). (C) A right maxilla of *Eocaecilia micropodia* (MCZ 9156) exhibiting a tentacular sulcus (ten s).

mon to representatives of all extant families: rhinatrematids (*Epicrionops*, Nussbaum, 1977, fig. 1), ichthyophiids (*Ichthyophis*, Taylor, 1969, figs. 2–7; Wake, 2003), uraeotyphlids (*Uraeotyphlus*, Nussbaum, 1979, fig. 1; *Uraeotyphlus narayani*, Wake, 2003, fig. 6B), scolecomorphids (*Crotaphatrema*, *Scolecomorphus*, Nussbaum, 1985, figs. 1, 4; *Scolecomorphus uluguruensis*, Wake, 2003, fig. 6E), caeciliids (*Caecilia*, *Oscaecila*, *Herpele*, Taylor, 1969, figs. 17–26, 42; *Oscaecilia ochrocephala*, Wake, 2003, fig. 9H; *Herpele*, Wake, 2003), and typhlonectids (*Typhlonectes*, *Potamotyphlus*, Taylor, 1969, figs. 12–14; *Typhlonectes natans*, Wilkinson and Nussbaum, 1997, fig. 9C). A few caeciliids exhibit an apparently derived condition in which the internal narial opening is completely surrounded by the palatine (maxillopalatine) (e.g., *Dermophis parviceps*, *Geotrypetes seraphini*, Taylor, 1969,

Figure 11. *Eocaecilia micropodia,* MNA V9346, ventral view of the palate, both stapes-quadrates and lower jaws.

figs. 30, 40, 41; *Dermophis mexicanus,* Wake and Hanken, 1982, fig. 2b; *Geotrypetes seraphini,* Wake, 2003, fig. 8E). In other species of *Dermophis,* however, both the vomer and palatine contribute to the narial margin (*D. glandulosus, D. occidentalis,* Taylor, 1969, figs. 31, 32). In various species of *Siphonops,* the internal naris is either variably bordered by the vomer and palatine or completely enclosed by the palatine (Taylor, 1969, figs. 36–39; Wake, 2003).

The pterygoid of *Eocaecilia micropodia* (Figs. 1, 3), together with the palatine and vomer, contributes to the relatively primitive configuration of the palate as a broad plate that laterally borders large interpterygoid vacuities. The articulation between the pterygoid and palatine, which is evident in the holotype where the two bones have partially separated from one another (Fig. 3), appears to have been composed of simple, overlapping surfaces. Both the quadrate ramus and the ascending process

of the pterygoid are preserved in MNA V9346 (Fig. 11). The elongate quadrate ramus has an extensive articulation with a sulcus on the inferior surface of the stapes-quadrate. In contrast to the condition in Recent caecilians, the quadrate ramus appears to have extended well posterior to the jaw articulation (cf. Figs. 1B, 3). Both the palatal ramus of the pterygoid and the parasphenoid component of the os basale are covered with pedicellate denticles. As reconstructed, the rostrocaudal length of the pterygoid in *Eocaecilia micropodia* is approximately half of the length of the skull, which is longer than in most (if not all) extant caecilians (see Taylor, 1969). Although a separate pterygoid persists in rhinatrematids and ichthyophiids, in typhlonectids and caeciliids the bone is ordinarily fused either to the quadrate or maxillopalatine (Nussbaum, 1977) or, in the case of scolecomorphids, possibly present only as a vestige (*Scolecomorphus vittatus,* Nussbaum, 1985, fig. 4) or lost altogether (*Crotaphatrema bornmuelleri,* Nussbaum, 1985, fig. 1; cf. Brand, 1956, for *Scolecomorphus uluguruensis*).

An ectopterygoid could not be identified in *Eocaecilia.* Nussbaum and Wilkinson (1989: 32) noted that a small "ectopterygoid" [sic] is present in some extant caeciliids. In *Gymnopis multiplicata* (Fig. 6C) and *Grandisonia alternans* (Taylor, 1969, figs. 34, 47), for example, this small bone forms the anteromedial palatal margin of the adductor chamber. Slight disarticulation of most skulls of *E. micropodia* has disrupted the palatal margins of the adductor chamber; in a few more intact specimens, the associated lower jaw is compacted against the region in which an ectopterygoid might be expected. The coronoid eminence, although low, extends anteriorly to approximately the midpoint of the jaw's length; if an ectopterygoid were present, the bone would have probably been much reduced in size so as not to impinge upon the coronoid eminence during jaw closure.

Os Basale. The braincase of *Eocaecilia,* as in all Recent caecilians, is constructed from two components: the os basale posteriorly and the sphenethmoid anteriorly. As in other caecilians, the os basale of *Eocaecilia* is a single bone that has been interpreted to represent a consolidation of ossification across a large area primitively occupied by separate bones (supraoccipital, exoccipitals, basioccipital, basisphenoid, pleurosphenoid, and parasphenoid). This massive element, which incorporates the otic capsules (presumably formed from the fusion of the prootic and opisthotic) as well as posterior elements of the endochondral braincase, is represented by numerous specimens (Figs. 2–5, 7, 11, 12, 15). In the holotype, the maximum width of the os basale, measured across the otic capsules, is estimated to be 3.5 mm; the estimated maximum length of the bone, which includes the cultriform process, is 10.4 mm.

Dorsally, the os basale has a sutural junction with the postparietals and forms a roof over the most posterior portion of the braincase and otic capsules; as in Recent caecilians, a median suture divides the two halves of the braincase above the foramen magnum (cf. Figs. 1, 2; Taylor, 1969). The dorsal surface of each half of the os basale in this region is slightly concave and bears fine, longitudinal striae, features that represent the attachment of epaxial muscles. A low ridge delineates the boundary between the skull's dorsal roof and occipital surface.

A complete occiput is represented only in the holotype, but certain details (such as the size and shape of the foramen magnum and the relative position of the occipital condyles) are distorted or obscured by postmortem compaction. Protuberant occipital condyles are preserved in two specimens (Figs. 13A, B, 15A, B, 16). The facets for the atlas are oval, slightly convex, face medially and slightly ventrally, and appear to have been situated ventral to the foramen magnum. A jugular foramen is present at the base of the occipital condyle (Fig. 3), closely approximating the ar-

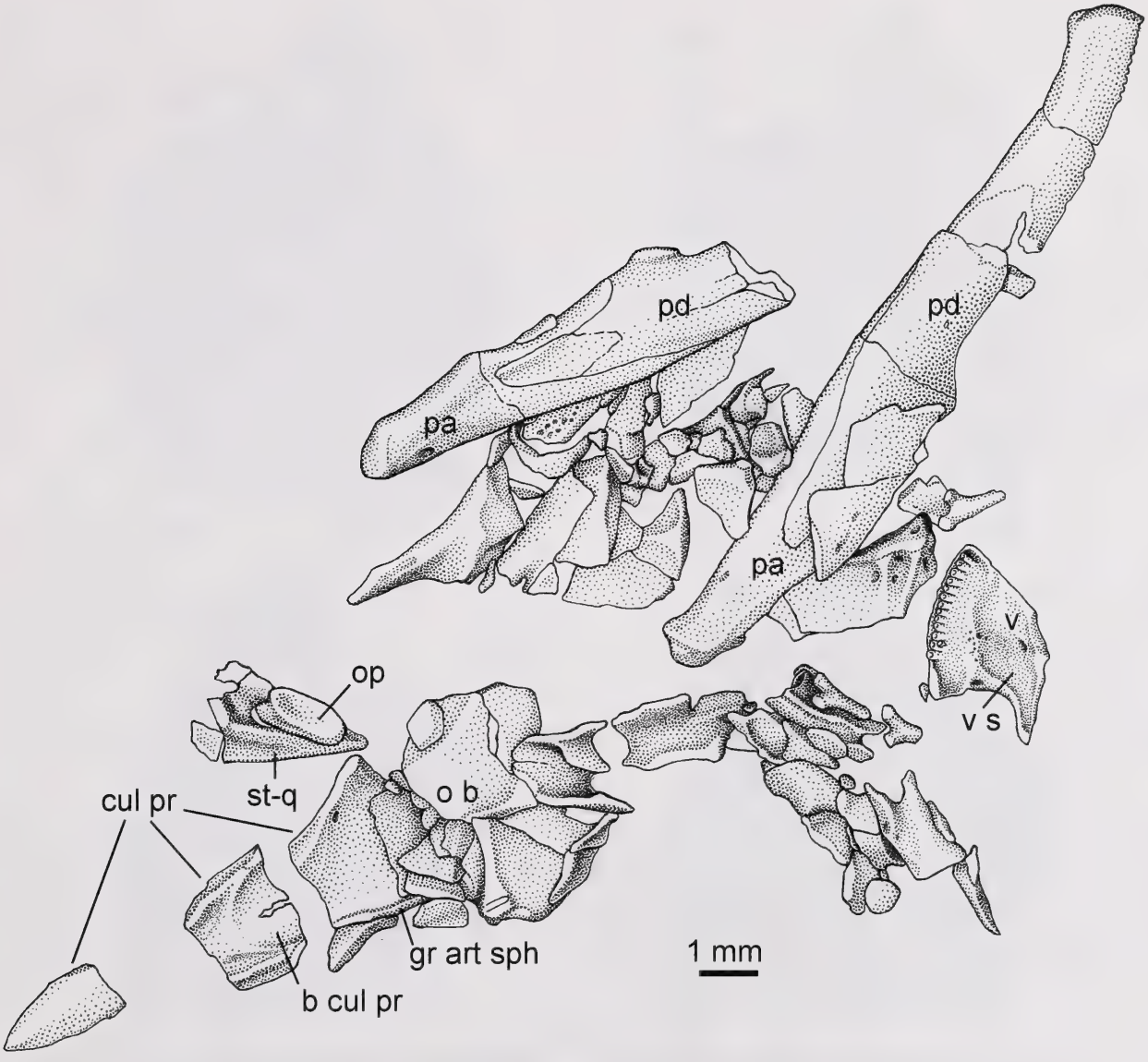
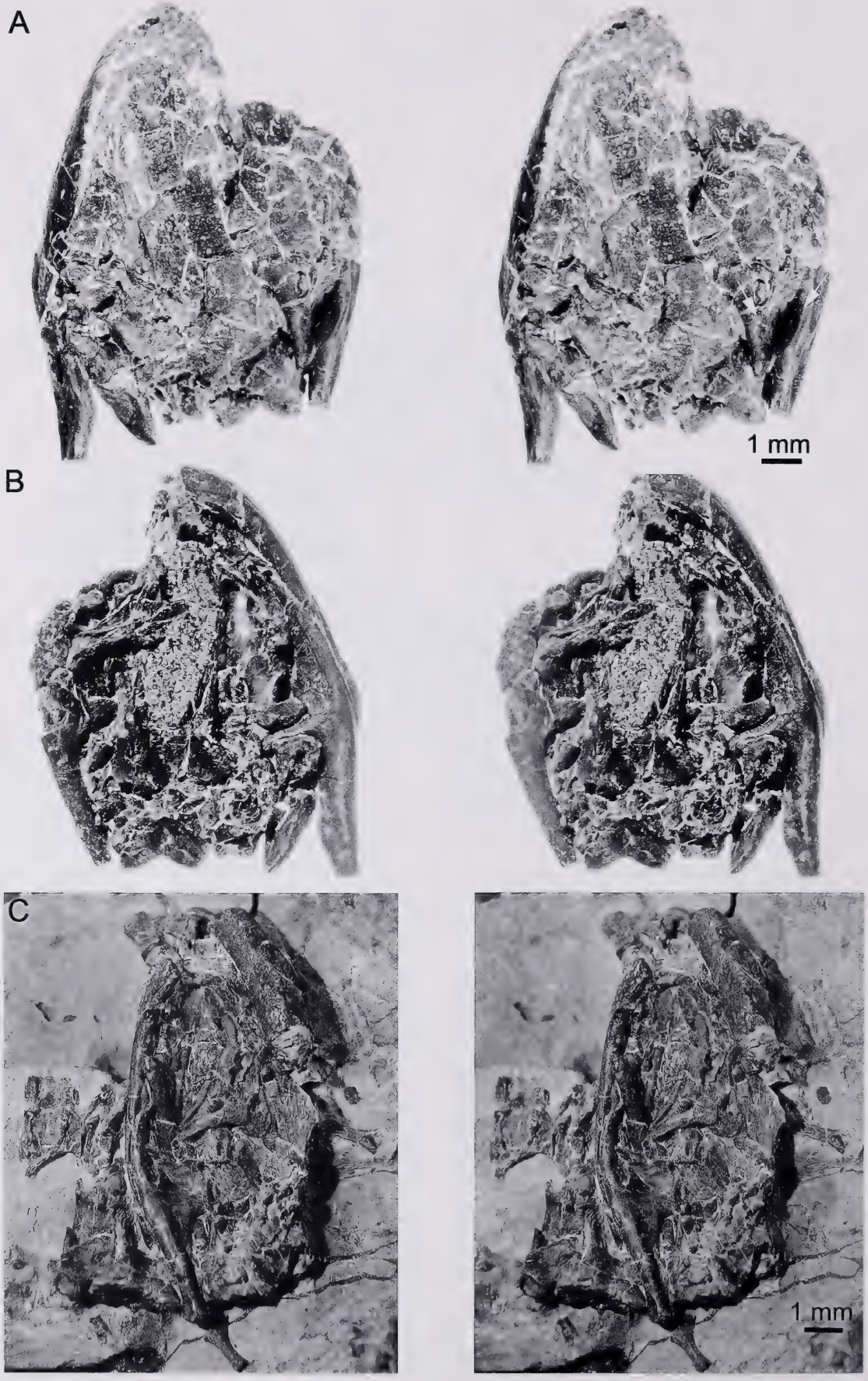


Figure 12. *Eocaecilia micropodia,* MCZ 9242, disarticulated elements of skull.

rangement in most modern forms. Slightly anteroventral to the jugular foramen is a small carotid foramen.

The ventral portion of the os basale incorporates the parasphenoid and is configured accordingly: posteriorly broad in the region of the otic capsules and anteriorly narrow in the region representing the cultriform process (Figs. 1B, 3). At the anterior border of the otic capsule, where the os basale narrows abruptly, one might expect to find a basicranial articulation with the pterygoid (as is common in Recent caecilians, Fig. 18E); no such articulation is discernible in *Eocaecilia* (Figs. 15A, 16, 17). The dorsal surface of the area representing the cultriform process bears a groove adjacent to the lateral margins for the articulation of the sphenethmoid (gr art sph, Fig. 12). The dorsal surface of the os basale is also marked by three depressions. The largest of these extends from the posterior margin of the braincase rostrally to the posterior terminus of the grooves for the sphenethmoid. At the rostral end of the depression is an elevated, hemicircular margin set transversely across the cultriform process that defines a very shallow basin (b cul pr, Fig. 12). Anterior to this depression are two additional shallow fossae, one on each side of the midline.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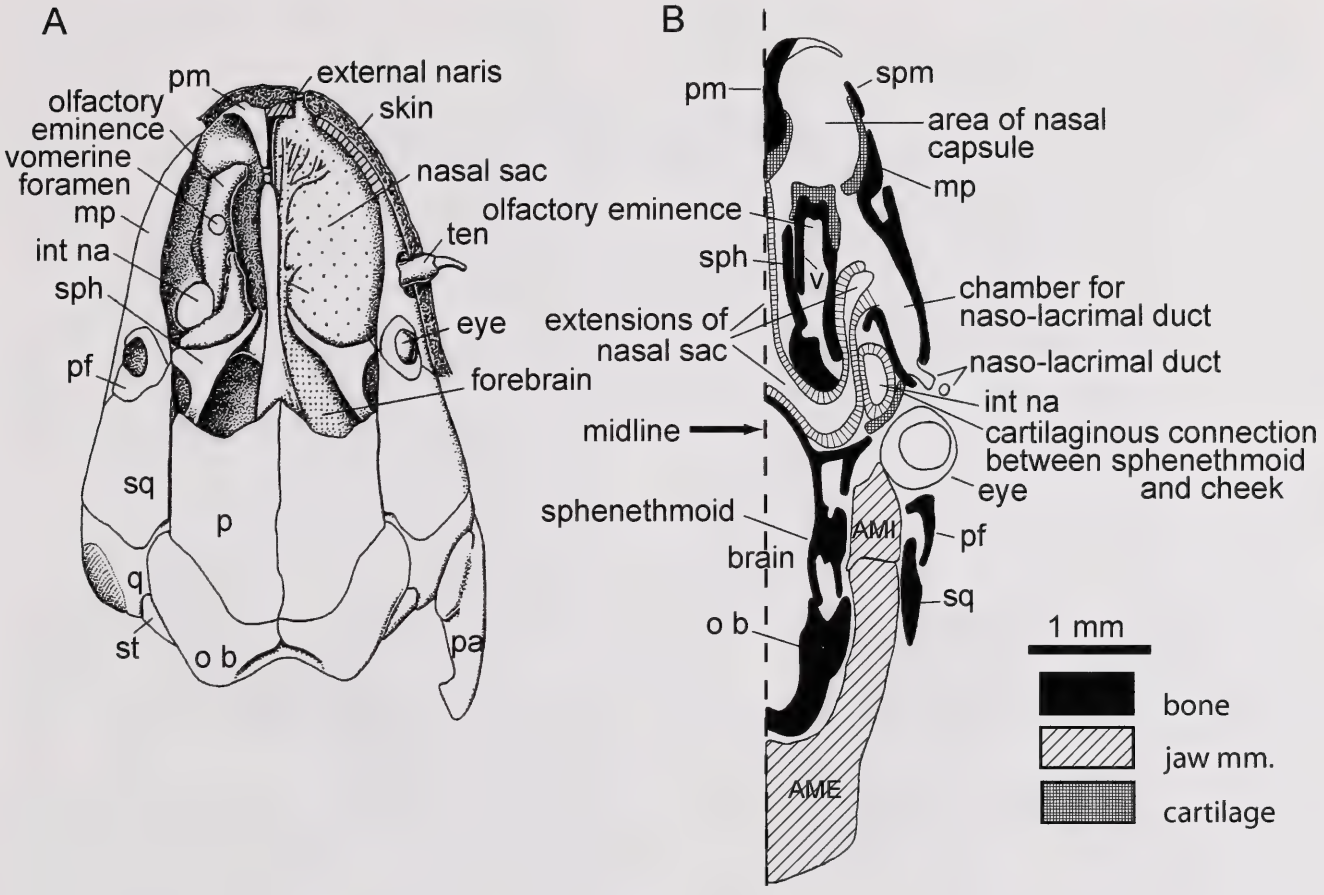

Figure 14. (A) The head of *Ichthyophis glutinosis* (FMNH 121528) in dorsal view, with skin and bones removed to reveal the extent of the nasal apparatus. The openly stippled area on the right side indicates the extent of the entire nasal sac. The finely stippled area indicates the forebrain and dorsal olfactory tract. On the left side, the nasal sac has been removed to expose the dorsal surface of bones underlying the nasal apparatus. (B) The head of *Epicrionops petersi* (LSUMZ 27324) in horizontal section (right side) to show the elaboration of nasal sac contents. The cartilages surrounding the area adjacent to the external nares are comparable in position and relative size to the entire nasal capsule in frogs, salamanders and Paleozoic amphibians.

The lateral aspect of the os basale, and specifically the otic capsule, is appressed to the massive stapes-quadrate; therefore, the structure of the capsule is best revealed by specimens in which the stapes-quadrate is missing or was removed (Figs. 15A–C, 16). An anterolaterally descending ridge marks the line of sutural contact with the skull roof (o r, Fig. 17A). The otic capsule of MNA V8063 is estimated to be approximately 2.0 mm in length and 1.6 mm in height. The lateral face of the otic capsule is dominated by a large fenestra ovalis which, in MNA V8063, is 1.4 mm in length and 0.6 mm in height. In MCZ 9169, the fenestra is irregularly oval in shape (length 1.7 mm; height 0.8 mm). The inferior margin is a gently convex, slightly thickened flange demarcating a narrow boundary between the external and internal surfaces of the capsule. The superior and posterior margins of the fenestra are broadly rounded, and the transition from the external to internal surface is more gradual.

The os basale bears a number of prominent foramina, the largest of which is lo-

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Figure 13. The skull of *Eocaecilia micropodia* (MCZ 9015) in (A) dorsal and (B) ventral views (stereophotographs). The jaw articulation between the stapes-quadrate and pseudoangular (arrows) is shown in the dorsal view. The ventral view reveals the extensive field of pedicels on the cultriform process. (C) A partial skull of *Eocaecilia micropodia* (MCZ 9237) in ventral view (stereophotographs).

cated at the anterior margin of the otic capsule, where the otic and pleurosphenoid regions join. On the basis of the comparable arrangement in modern caecilians (in particular, *Dermophis mexicanus*), this foramen is presumed to convey cranial nerve V (Fig. 15B). A second foramen lies at the anterolateral margin of the otic capsule, slightly ventral and lateral to that for V; elevated on a slight eminence, this foramen is interpreted as the exit of cranial nerve VII (Fig. 15B, C). A third, small foramen opens onto the posterolateral margin of the parasphenoid portion of the os basale and is confluent with a long sulcus on the lateral surface of the parasphenoid; both features are interpreted as representing the passage of the carotid artery (Fig. 15B).

Although the overall configuration of the os basale of *Eocaecilia micropodia* is comparable to that in living caecilians, differences are apparent in a number of details. First, the shape of the cultriform process is distinctive (cf. Figs. 1, 3, 6). Illustrations of the palates of modern caecilians by Taylor (1969) and Wake (2003) reveal a diversity of cultriform process outlines, none of which is especially similar to that of *E. micropodia*, which is elongate (relative to skull length) and narrow. The constricted posterior end of the cultriform process is distinctly demarcated from the broad capsular part of the os basale. Finally, the lateral margins of the process, rather than converging at an acute angle as in many living taxa, remain subparallel for much of their length and converge distinctly only near the apex.

Second, the palatal surface of the cultriform process bears an irregular array of pedicellate teeth (although no specimen preserves a tooth crown in place). The diameters of the pedicel bases on the cultriform process are more variable and, on average, smaller than those found on the jaws. On the type specimen (MNA V8066, Fig. 3), a sample of 14 well-preserved pedicels range from 0.07 to 0.13 mm in diameter; the mean of 0.09 mm is less than the means of 0.11–0.12 mm observed from tooth rows of the upper and lower jaws. On MNA V8071, a sample of eight pedicels on the cultriform process has a mean diameter of 0.1 mm, whereas the estimated diameters of several poorly preserved pedicels on the associated mandible is 0.13 mm.

Third, the condyles and the facets in *Eocaecilia micropodia* are relatively smaller than those of gymnophionans. An index of the relative size of the atlanto-occipital articulation is the bilateral breadth of the condyles (the distance between the lateral margins of the two condylar facets) expressed as a percentage of skull width. The specimen of *E. micropodia* in which the condyles appear undistorted (MCZ 9015, Fig. 13B) reveals their bilateral breadth to be 25% of the skull width. Indices taken from MCZ gymnophionan specimens or the literature reveal a range of values between 33 and 45%: the rhinatrematid *Epicrionops petersi*, 39% (Nussbaum, 1977, fig. 1); the uraeotyplid *Uraeotyphlus narayani*, 41% (Nussbaum, 1979, fig. 1); the typhlonectid *Typhlonectes compressicauda*, 33% (MCZ 24524); the ichthyophiid *Ichthyophis glandulosus*, 34% (MCZ 14003); the scolecomorphid *Scolecomorphus uluguruensis*, 39% (MCZ 12284); and various caeciliids: *Afrocaecilia taitana*, 45% (MCZ 20021); *Dermophis mexicanus*, 38% (MCZ 126357); *Gegeneophis ramaswamii*, 38% (MCZ 29456); *Geotrypetes seraphini*, 42% (MCZ 3424); *Gymnopis multiplicata*, 36% (MCZ 29265); *Oscaecilia ochrocephala*, 40% (MCZ 9591); *Schistometopum gregorii*, 39% (MCZ 20070); and *Siphonops annulatus*, 36% (MCZ 19402).

The articular facets of *E. micropodia* are relatively small as well. In MCZ 9015, the greatest width of a facet (measured along the long axis of the oval) is 0.7 mm, or 10% of the estimated skull width of 7.2 mm compared with values of 15% in *Siphonops annulatus* (MCZ 19405), and 17% in *Gegeneophis ramaswamii* (MCZ 29452)

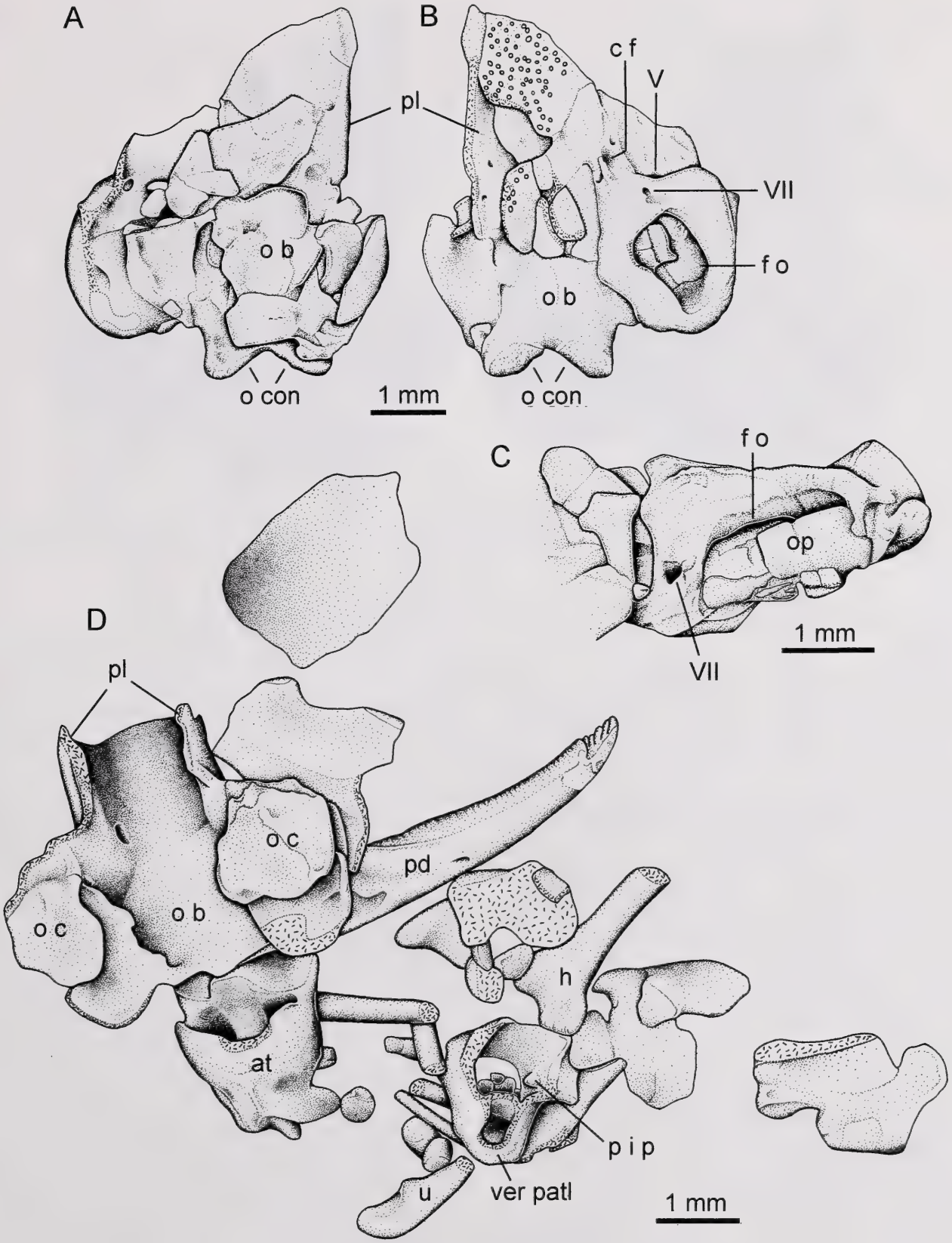

Figure 15. The os basale of *Eocaecilia micropodia* (MNA V8063) in (A) dorsal and (B) ventral views. For stereophotographs of this specimen in ventral view, see Figure 16. (C) An otic capsule (MCZ 9169) in lateral view exhibiting the fenestra ovalis and associated operculum. (D) A partial braincase and the otic capsules in ventral view (MCZ 9167).

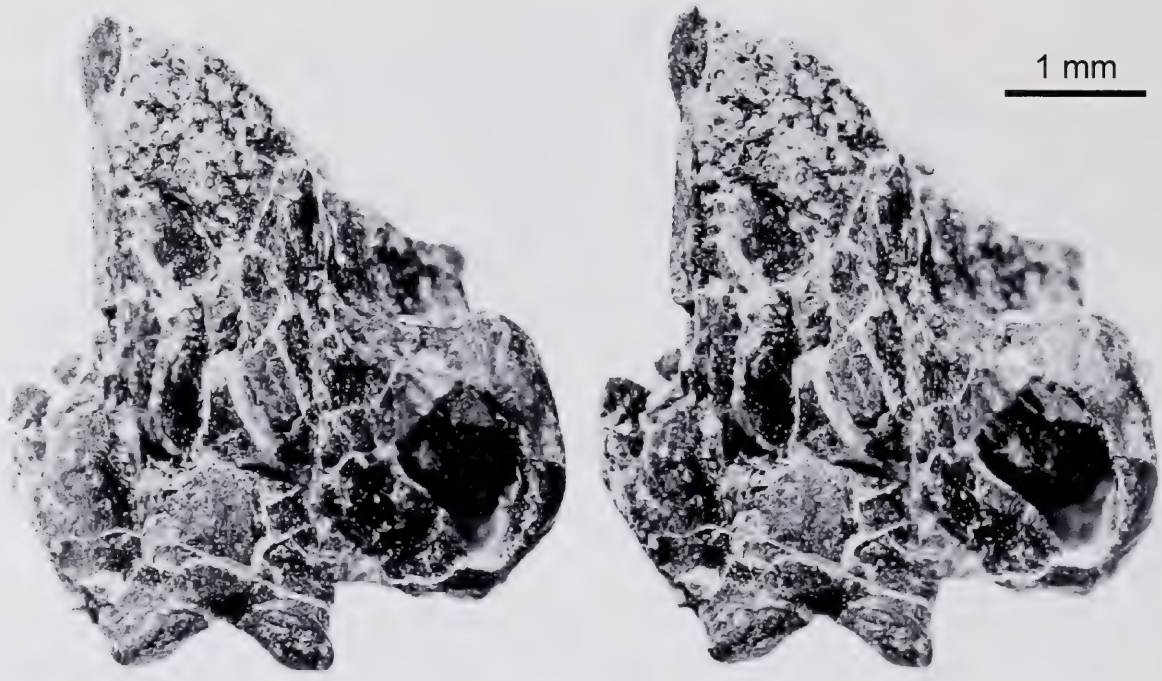

Figure 16. The braincase of *Eocaecilia micropodia* (MNA V8063) in ventral view (stereophotographs). For labeled drawings of this specimen, see Figure 15A, B.

and *Typhlonectes compressicauda* (MCZ 24524).

A fourth difference is that the ventral aspect of the os basale of *Eocaecilia micropodia* lacks any indication on its ventral surface of the attachment of subvertebral cranial depressor musculature, specifically the longus capitis. In many Recent caecilians, a pair of facetlike depressions anterior to the foramen magnum, separated in the median plane by a low ridge, mark this attachment site (cf. Figs. 3, 6B–D). The muscle flexes the skull ventrally, a movement that Bemis et al. (1983) suggested would be employed in both feeding and burrowing.

Pleurosphenoid. Anteromedial to the otic capsule a large pleurosphenoid forms the lateral wall of the braincase, extending anteriorly along the lateral margin of the parasphenoid portion of the os basale toward the sphenethmoid (Fig. 16), as in modern caecilians. The pleurosphenoid does appear to have been fully fused to the parasphenoid (Figs. 15, 16). In MCZ 9167, the pleurosphenoid is approximately 3.4 mm long and 1.9 mm high. The anterior margin of the pleurosphenoid is recessed, and a small gap, estimated to be 1.4 mm in width, separates the anterior margin of this bone from the posterior margin of the sphenethmoid (Fig. 17A). This gap is likely to have accommodated the egress of cranial nerves II, III, and IV.

Sphenethmoid. The sphenethmoid of *Eocaecilia micropodia,* which is not well preserved or visible in its entirety in any one specimen, is reconstructed (Fig. 17) on the basis of the holotype, MNA V8066, and MNA V8059 (Fig. 7). The sphenethmoid appears to conform generally to the pattern in modern caecilians (Fig. 18). In the holotype, the sphenethmoid is estimated to be 3.8 mm in length, or approximately half of the length of the parasphenoid portion of the os basale. This well-ossified, complex element represents the rostral end of the braincase. The posterior half of the sphenethmoid forms the thin lateral walls of the anterior part of the braincase (the walls of the posterior part of the braincase are contributed by the pleurosphenoids, Fig. 17A). The anterior end of the sphenethmoid is a robust, expanded structure that forms the transverse posterior wall of the nasal chambers. As in

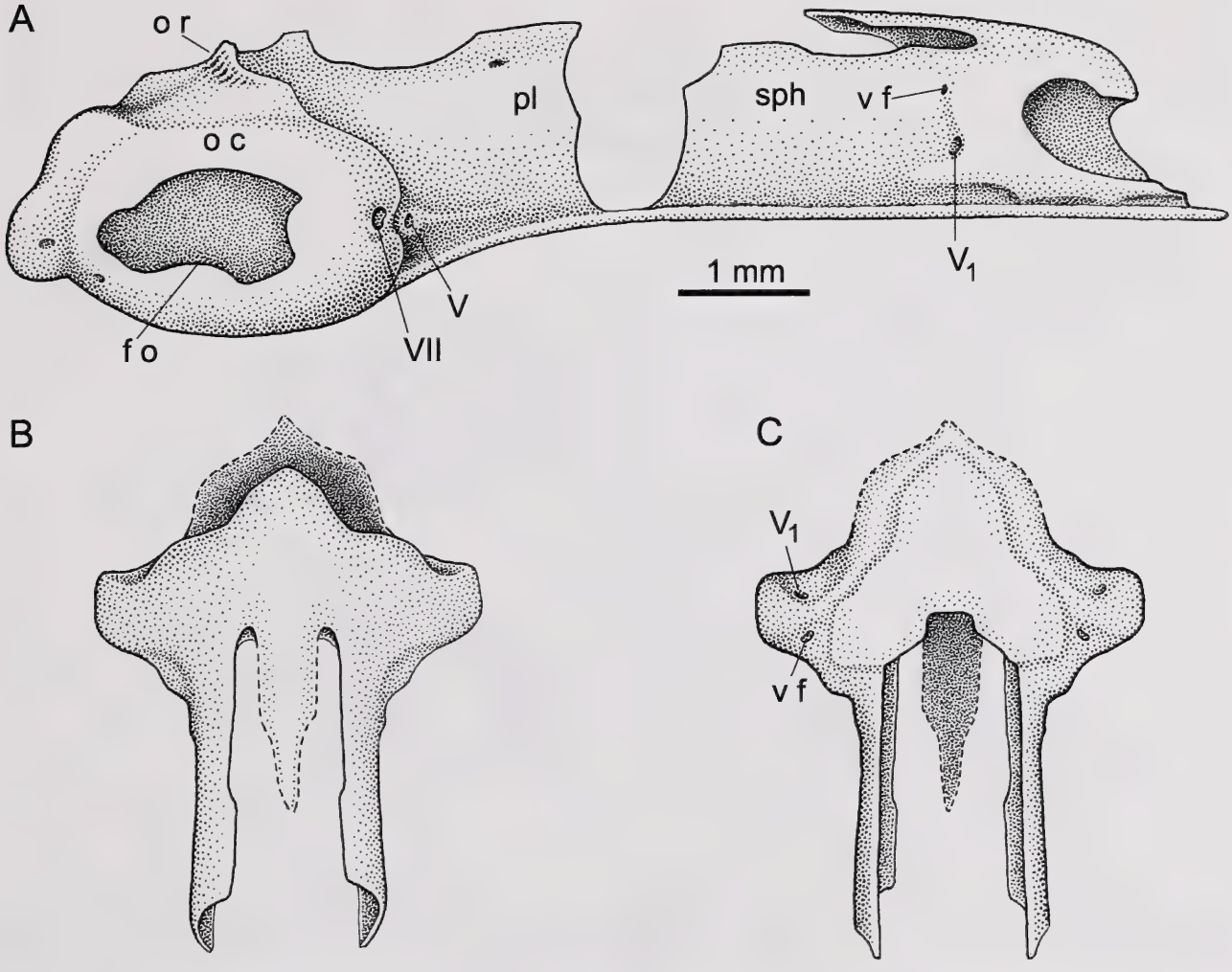

Figure 17. (A) Reconstruction of the braincase in *Eocaecilia micropodia* in lateral view. The reconstruction is based on the holotype (MNA V8066; Figs. 2, 3) and MNA V8059 (Fig. 7). The sphenethmoid (sph) component of the braincase in (B) dorsal and (C) ventral views.

modern taxa, the bone serves a supporting role in the anterior portion of the skull by extending dorsoventrally from the cultriform process of the os basale to the ventral surface of the skull roof. The sphenethmoid is not exposed dorsally as a component of the skull roof, nor is it in most Recent caecilians: rhinatrematids (e.g., *Epicrionops,* Nussbaum, 1977, fig. 1; Wake, 2003, fig. 5A), ichthyophiids (*Ichthyophis* sp., Wake, 2003, fig. 5G), uraeotyphlids (*Uraeotyphlus narayani,* Wake, 2003, fig. 6A), scolecomorphids (*Scolecomorphus uluguruensis,* Wake, 2003, fig. 6D), and typhlonectids (*Typhlonectes compressicauda* and *T. natans,* Wake, 2003, fig. 6G, J; *Potomotyphlus kaupii,* Wilkinson and Nussbaum, 1997, fig. 8B; see also Taylor, 1969; Wiedersheim, 1879). Dorsal exposure of the sphenethmoid does occur in various extant caeciliids in which the bone appears as a median element between the frontals (Taylor, 1969; Wake, 2003). The anterior portion of the sphenethmoid of *E. micropodia* also extends toward the lateral margin of the skull. In *Epicrionops,* the sphenethmoid continues as a cartilaginous posterior wall of the narial passage (Fig. 14B), possibly adding an additional buttress against the compressive forces of burrowing. The same process occurs in *Ichthyophis* (the lamina orbitonasalis of Visser, 1963).

The sphenethmoid in *Eocaecilia micropodia* is pierced by several foramina. One, located on the posterior face of the lateral

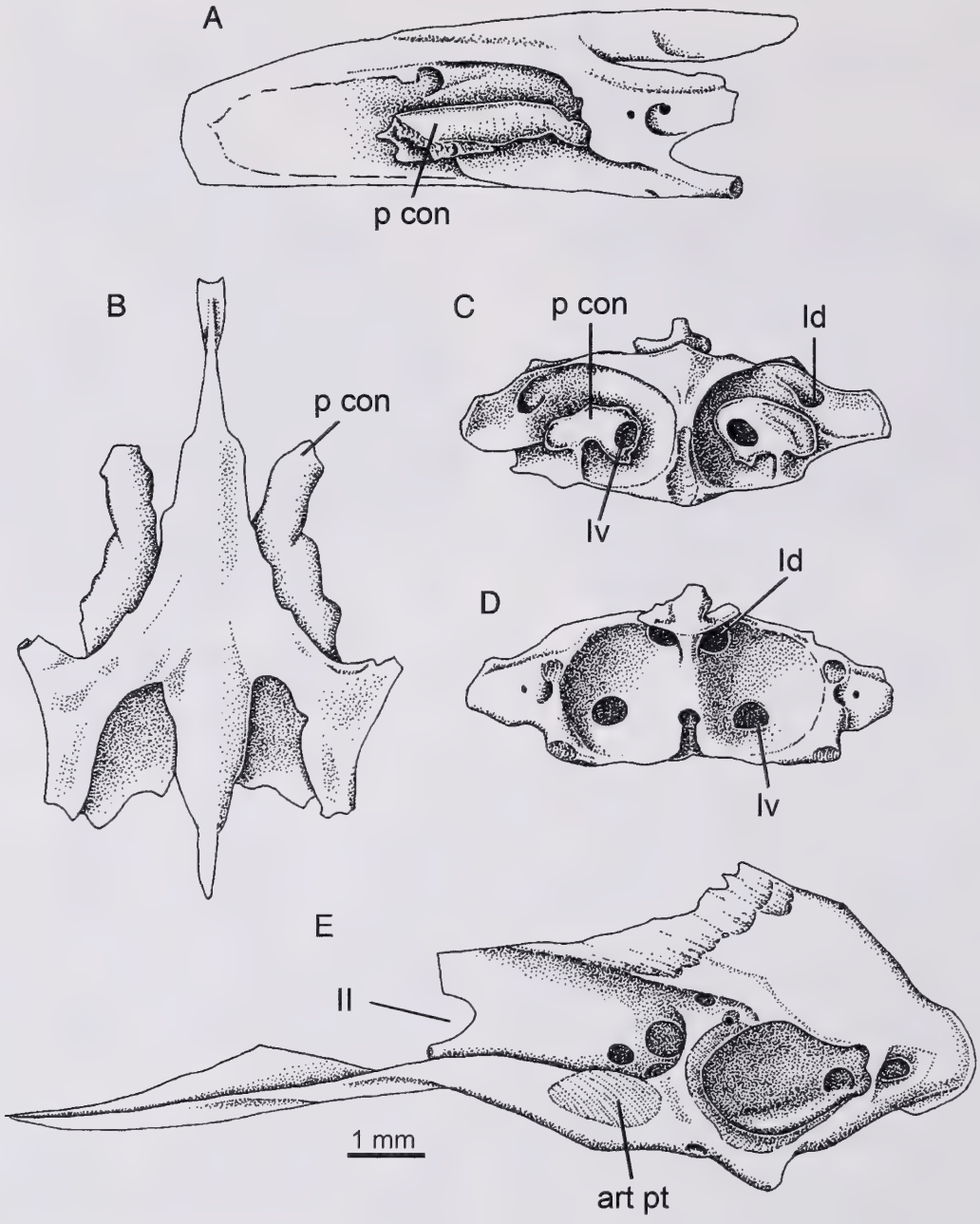

Figure 18. Braincase of *Dermophis mexicanus* based on a specimen described by Wake and Hanken (1982) in the collection of Marvalee H. Wake, Department of Integrative Biology, University of California, Berkeley. Sphenethmoid in (A) left lateral, (B) dorsal, (C) anterior, and (D) posterior views. (E) Os basale in left lateral view.

wing (Figs. 1B, 3; V_1, Fig. 17A, C) is comparable in position to a foramen in Recent taxa (e.g., *Ichthyophis*) that conveys the deep ophthalmic branch of cranial nerve V. Another foramen, visible in both lateral and ventral aspects (v f, Fig. 17A, C), enters the sphenethmoid at a level slightly above the opening for deep ophthalmic branch and is interpreted (by comparison with *Ichthyophis*) to represent a vascular foramen.

Stapes-quadrate. Although the skull and lower jaw of *Eocaecilia micropodia* resemble those of Recent caecilians in many aspects, the structure of the stapes and jaw suspension is unlike that in any other known gymnophionan and, furthermore, appears to have no parallel among other terrestrial vertebrates. There is a single element situated in the stapedial and quadrate region that has characteristics of both bones. As would be expected of a quad-

rate, the bone is firmly attached to the skull in three areas: posteroventrally to the quadrate ramus of the pterygoid (Fig. 11), dorsally to the back of the skull table (Figs. 1A, C, 2), and anteriorly to the underside of the squamosal (Figs. 5, 19B). Furthermore, the bone bears a distinct facet for articulation with the lower jaw (Figs. 13A, 19B, 20D, 21C). As would be expected of a stapes, the bone is closely associated with the otic capsule and is traversed by a relatively large foramen; the size of the foramen is consistent with a vascular passage (i.e., a stapedial artery, Figs. 2, 11, 19–21) rather than a narrow conduit expected for a nerve (such as the chorda tympani, which traverses the quadrate). The nature of the attachment to the otic capsule, however, is less well defined than in Recent caecilians, in which the thickened edges of the footplate (e.g., in *Dermophis mexicanus*, Fig. 22) articulate with the margins of the fenestra ovalis. This large and complexly shaped single element can be termed a stapes-quadrate, although there is no evidence of sutural fusion in any specimen. Nearly all aspects of the stapes-quadrate can be seen in one or more specimens, yet in no single specimen is the entire bone both complete and fully exposed; integrating a reconstruction (Fig. 21) proved difficult and required certain simplifications to be consistent in all views.

The stapes-quadrate is a large bone (approximately one-third of the skull length) that extends, as a posterior process, behind the dermal skull roof and between the retroarticular process of the lower jaw and the otic region of the os basale (Fig. 2). Although the posterior process of the stapes-quadrate resembles the stem or shaft of a stapes (by analogy with those in Paleozoic tetrapods; cf. Lombard and Bolt, 1988, figs. 3–9), its medial surface lies lateral to the fenestra ovalis and thus occupies a position that would be expected of a footplate. Rather than fitting into the fenestra ovalis, as in modern caecilians (Fig. 10B), the medial surface is large enough to have completely overlapped the margins of the fenestra. However, in the type, which is the least distorted specimen, neither stapes-quadrate lies in intimate contact with the fenestra ovalis (Fig. 3). The presence of an ossicle in this region (see below, *Operculum*) is additional evidence favoring the interpretation that the stapes actually had withdrawn from contact with the otic region (and assumed principally a jaw suspensory function and only secondarily, by bone conduction, an auditory function). The caudal end of the posterior process of the bone is free (i.e., lacks any bony contact). The lateral surface of the distal end of the process is rugose; the rugosity is slightly raised along the dorsolateral margin of the process and could represent evidence of tendinous attachment. The adjacent medial surface of the lower jaw's retroarticular process is also rugose.

A deep, triangular fossa on the anterior surface of the stapes-quadrate (Figs. 20C, 21E), medial to the area of articulation with the lower jaw and dorsolateral to the articulation with the quadrate ramus of the pterygoid, represents an extension of the adductor chamber. The anterodorsal portion of the stapes-quadrate extends rostrad as a narrow lamina (Fig. 21A–D) that contributes to the lateral margin of the adductor chamber. We interpret the rugosity on the dorsal surface of the lamina as an area of attachment to the undersurface of the lower margin of the cheek.

A large stapedial foramen traverses the bone obliquely from dorsolateral to medial surfaces in a ventromedial and somewhat posterior direction (Figs. 2, 11, 19–21). Laterally, the foramen is distinctly oval (the long and short diameters of which measure 0.4 and 0.2 mm in MNA V8066; in MCZ 9169, the diameters are 0.5 and 0.25 mm, respectively); medially, the foramen is nearly circular. The foramen opens onto the concave medial surface of the posterior process in a position slightly rostral to the fenestra ovalis. Rostral to the foramen's dorsolateral opening, an anterodorsal extension of the stapes-quadrate apparently attaches to the underside of the

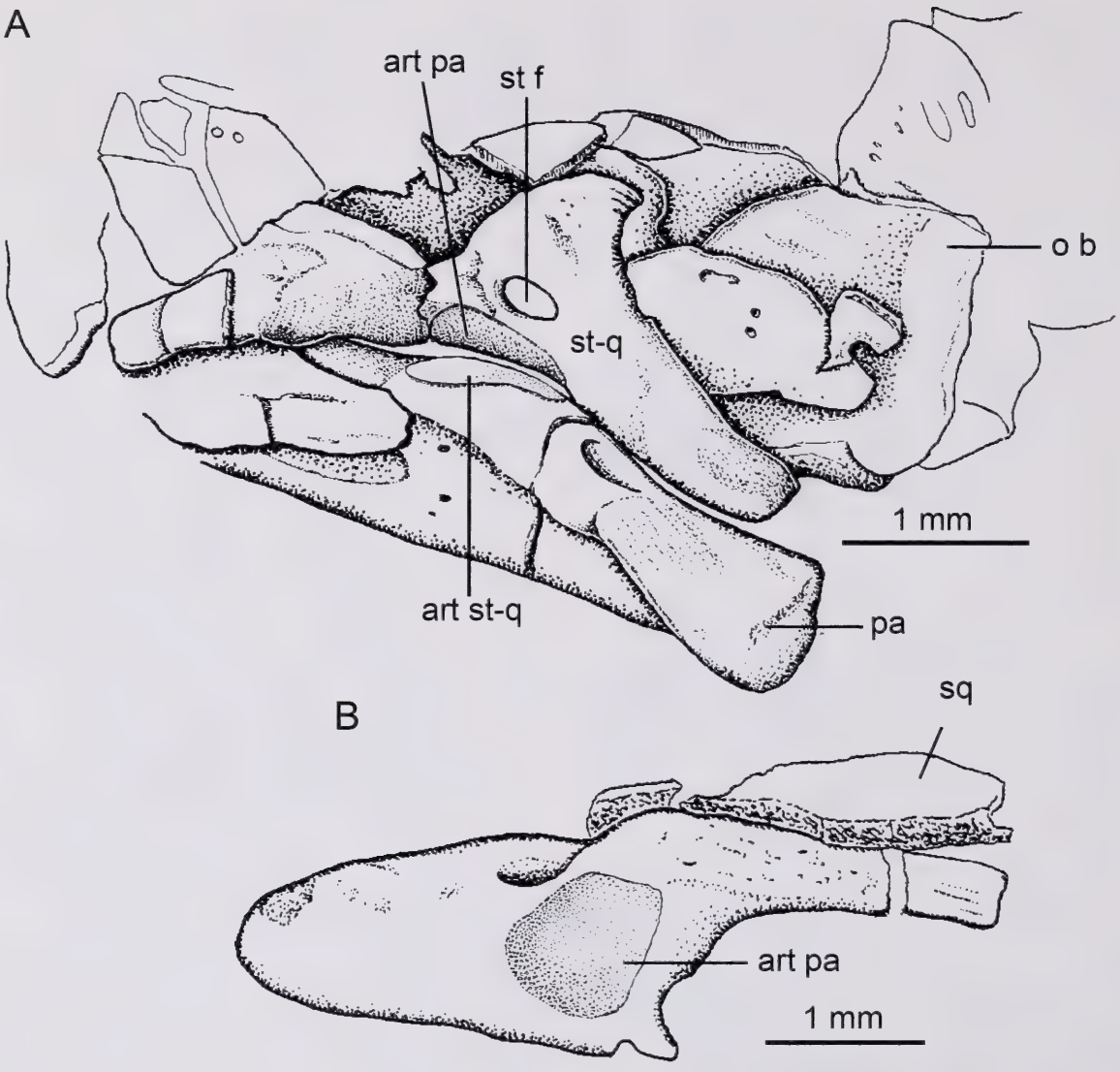

Figure 19. Stapes-quadrates of *Eocaecilia micropodia*. (A) Left side of the type specimen (MNA V8066) in oblique posterolateral view, showing articulation with pseudoangular. (B) Lateral view of right stapes-quadrate of MCZ 9169.

skull roof, near or at the occipital margin (a relationship preserved only in the holotype, Fig. 2).

An approximately oval articular facet is situated at the middle of the lateral surface of the stapes-quadrate (Figs. 19B, 21C). In MCZ 9235, the dimensions of the facet in the anteroposterior and dorsoventral planes are, respectively, 1.1 and 0.8 mm; comparable dimensions are seen in MCZ 9169 (1.1, 0.9 mm). The jaw joint is formed by the apposition of this facet with another on the medial surface of the pseudoangular (Figs. 19A, 24C, 26B; see also Jenkins and Walsh, 1993, fig. 1e). The surfaces of both facets are of "unfinished" bone, evidence of a cartilaginous covering and a synovial joint. The facet on the stapes-quadrate faces principally laterally but is inclined slightly ventrally (Fig. 29A); the relatively flat surface, which exhibits a very shallow anteroposterior concavity, contrasts markedly with the complexly configured quadrate and pseudoangular facets in Recent gymnophionans (Fig. 29B, C). Anterior to this facet is a rounded, transverse bar that forms the posterior margin of the adductor chamber; relative to the lower jaw, the bar is positioned at a point just posterior to the insertion of the adductor muscles. The finished surface of the bone lacks any indication of articular cartilage;

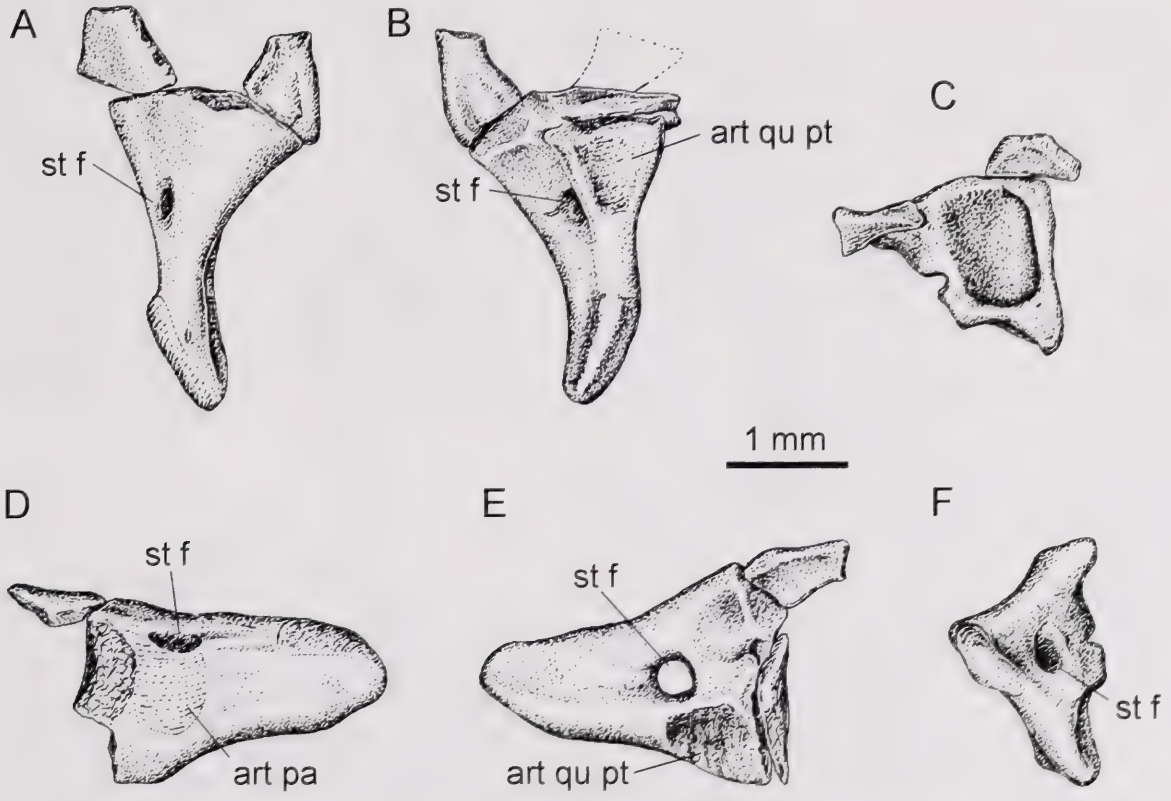

Figure 20. Left stapes-quadrate of *Eocaecilia micropodia,* MCZ 9169. (A) dorsal, (B) ventral, (C) anterior, (D) lateral, (E) medial, (F) posterior views.

therefore, the bar appears not to be a component of the jaw joint.

In most gymnophionans the quadrate and stapes retain separate identities. The apparent fusion of the stapes-quadrate in *Eocaecilia micropodia* represents a more derived condition than that of some Recent caecilians in which the quadrate and stapes are closely abutted and even articulate by means of a synovial joint. In a juvenile *Ichthyophis glutinosus,* for example, de Jager (1939b) described a synovial joint between the stapes and quadrate. Serial sections of adult *Ichthyophis glutinosus* (Fig. 23) and a specimen of *Epicrionops petersi* examined by R.L.C. confirm an extensive contact between the quadrate and stapes. Yet *E. micropodia* is not unique among known caecilians for having completely departed from the ancestral condition of a distinct stapes and quadrate. Scolecomorphids lack stapes as well as foramina ovales (Nussbaum, 1985). Specimens of *Boulengerula boulengeri* were reported by de Villiers (1936, 1938) to variably exhibit a synovial articulation between the stapes and quadrate or partial fusion of the two bones. de Jager (1939a) described an incipient fusion of the stapes and quadrate in *Dermophis mexicanus,* but this condition was not confirmed by Wake and Hanken (1982: 214), who reported that "the stapes is always free of the quadrate. . . ." In *D. mexicanus,* however, the quadrate fuses with the pterygoid (Wake and Hanken, 1982), a condition that Lawson (1963) believed to be present in *Hypogeophis rostratus.*

The massive stapes-quadrate, intimately articulated with the quadrate ramus of the pterygoid and functioning in the jaw articulation, presumably could have transmitted vibrations by bone conductance. Stapes in Recent caecilians serve both auditory and structural roles, linking the braincase (otic capsule) with the cheek (quadrate). Although the modern caecilian stapes is not a component of an impedance matching system, as in amniotes and most frogs, the apparatus does respond to low-

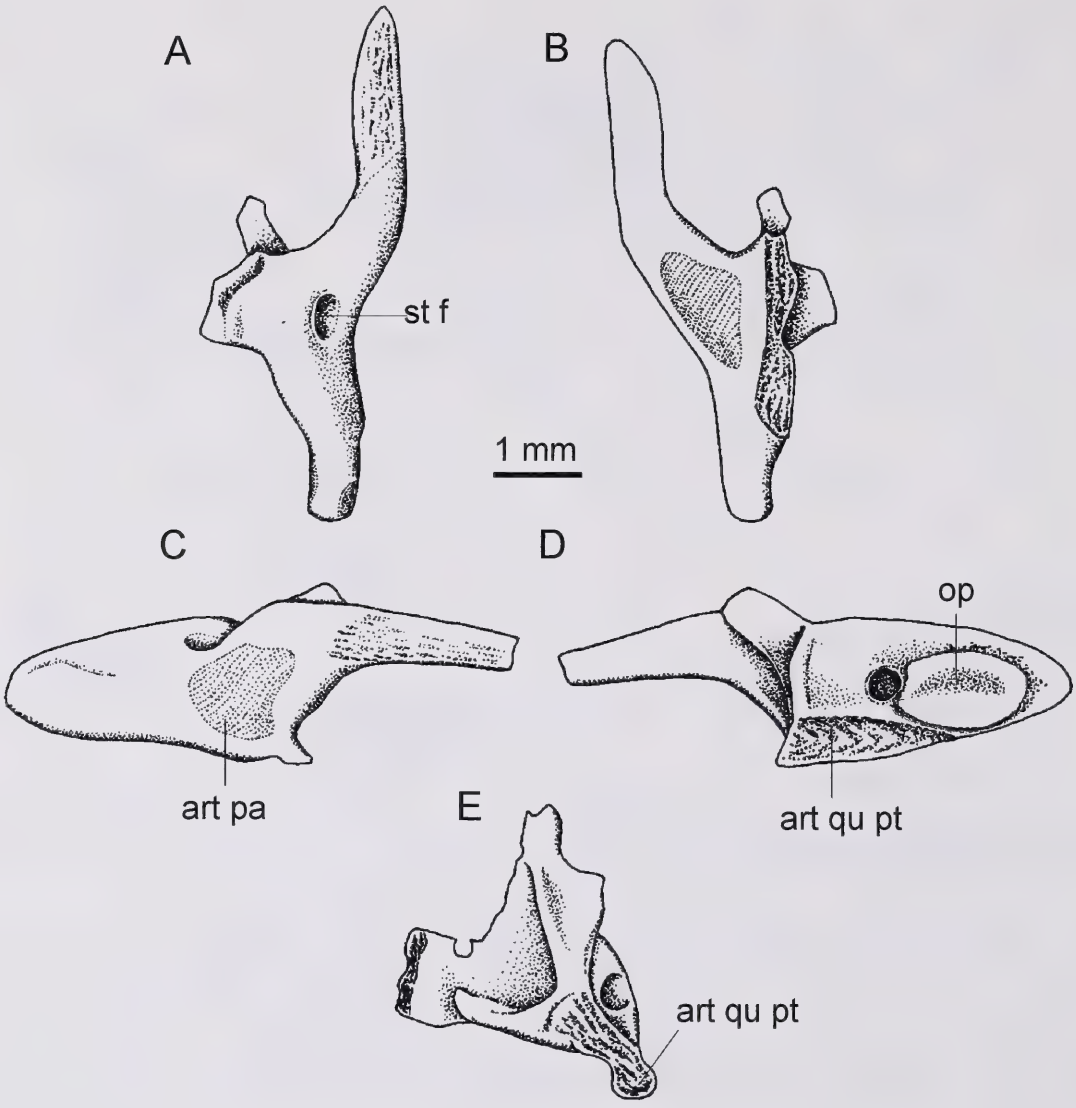

Figure 21. Reconstruction of the right stapes-quadrate of *Eocaecilia micropodia* based on MCZ 9169 and MNA V8066, V9346. (A) dorsal, (B) ventral, (C) lateral, (D) medial, (E) anterior views (E drawn from MNA V8059).

frequency vibrations (Wever, 1975; Wever and Gans, 1976).

Operculum. An ossicle is preserved with several specimens, either in proximity to the fenestra ovalis or stapes-quadrate, or in isolation. In MCZ 9242 (op, Fig. 12) and MNA V8054 (Fig. 25G) the ossicle is a thin, oval plate resting against the stapes-quadrate. The medial surface facing the fenestra ovalis is concave. In both MCZ 9242 (Fig. 12) and the holotype, the edges are thickened, as in the case of gymnophionan stapedial footplates that articulate with the margins of a fenestra ovalis (Fig. 22). In MCZ 9156 (Fig. 9), the ossicle lies against the retroarticular process, close to the jaw articulation. In the holotype (Fig. 3), the ossicle appears to have been turned outward and lies immediately adjacent to the fenestra ovalis. The variable positions in which the ossicle is preserved are evidence that this element was not rigidly attached but presumably was anchored by soft tissue. In MCZ 9169 (Fig. 15C), however, the ossicle was exposed by removal of the stapes and, although fragmented, was found to be closely associated with the fenestra ovalis; the reconstructed shape of the ossicle is an elongate oval that would have occupied most or all of the fenestra ovalis, the margins of which are well preserved.

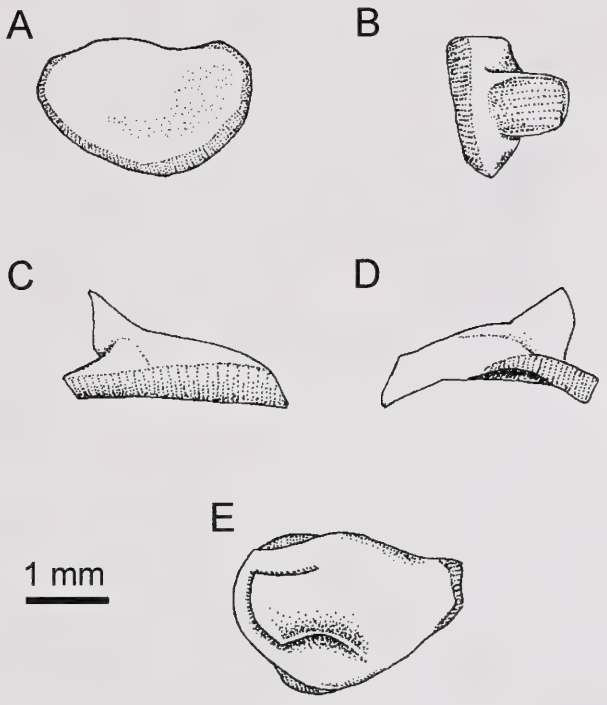

Figure 22. Stapes of the *Dermophis mexicanus* in (A) medial, (B) anterior, (C) ventral, (D) dorsal, and (E) lateral views. Drawn from a specimen described by Wake and Hanken (1982) in the collection of Marvalee H. Wake, Department of Integrative Biology, University of California, Berkeley.

The oval shape and otic association of the ossicle of *Eocaecilia micropodia* are comparable to that found in the opercula of frogs (Wever, 1973) and salamanders (Monath, 1965), and on this evidence, the ossicle can be proposed as a homologous opercular element. Unlike Recent caecilians, *E. micropodia* retained a shoulder girdle to which an operclaris muscle could have attached. No extant caecilian is known to have an operculum. Duellman and Trueb (1986: 387) state that the operculum in caecilians is either absent or fused with the footplate of the stapes and elsewhere (1986: 306) cite Marcus (1935) as suggesting that the operculum in *Hypogeophis* ". . . has been incorporated into the stapedial footplate, as . . . in plethodontid salamanders." However, Marcus actually made no so such claim, having been unable to identify any vestige of an operculum in his developmental study: "Von einem operculum finde ich auch in der Entwicklung keine Spur" (Marcus, 1935: 145). Although Marcus (1935) did suggest that part of the otic capsule is incorporated into the stapedial footplate in *Hypogeophis*, Wake and Hanken's (1982) study of *Dermophis mexicanus* revealed only a single ossification center for the stapes, with no evidence of a separate origin for the footplate. On the basis of the limited evidence available, we conclude that the operculum in Recent gymnophionans has been lost.

An assessment of the possibility that the ear ossicle in *Eocaecilia micropodia* is actually a reduced stapes, rather than an operculum as here interpreted, can only be made with reference to structures in putatively basal gymnophionans (i.e., the rhinatrematids *Epicrionops* and *Rhinatrema*; Nussbaum, 1977, 1979; Wilkinson, 1992, 1996; Wilkinson and Nussbaum, 1996). In these forms, the stapes is a relatively massive bone that fits tightly into the margins of the fenestra ovalis; a rostrally directed stem articulates via a synovial joint with the posterior surface of the quadrate, and a stapedial foramen traverses the base of the stem. Although the stapes-quadrate of *E. micropodia* possesses a stapedial foramen, the bone does not "fit" within the fenestra ovalis. Postmortem distortion obviates the possibility of determining whether the stapes-quadrate contacted or simply lay in close apposition to the otic capsule. Certainly the concave medial surface of the posterior process of the stapes-quadrate exhibits no structural feature that would conform to the fenestral aperture. Two interpretations are therefore possible. First, the ear ossicle of *E. micropodia* is a reduced stapes, and the correspondingly enlarged quadrate has captured the course of the stapedial artery. Alternatively, the ossicle is a true operculum, and the stapes retained the primitive relation to the stapedial artery but lost the primitive seating of a footplate within the fenestra ovalis. We favor the latter interpretation on several grounds. Given the intimate association of stapes and quadrate in numerous extant taxa, the fusion of these two elements is not an altogether

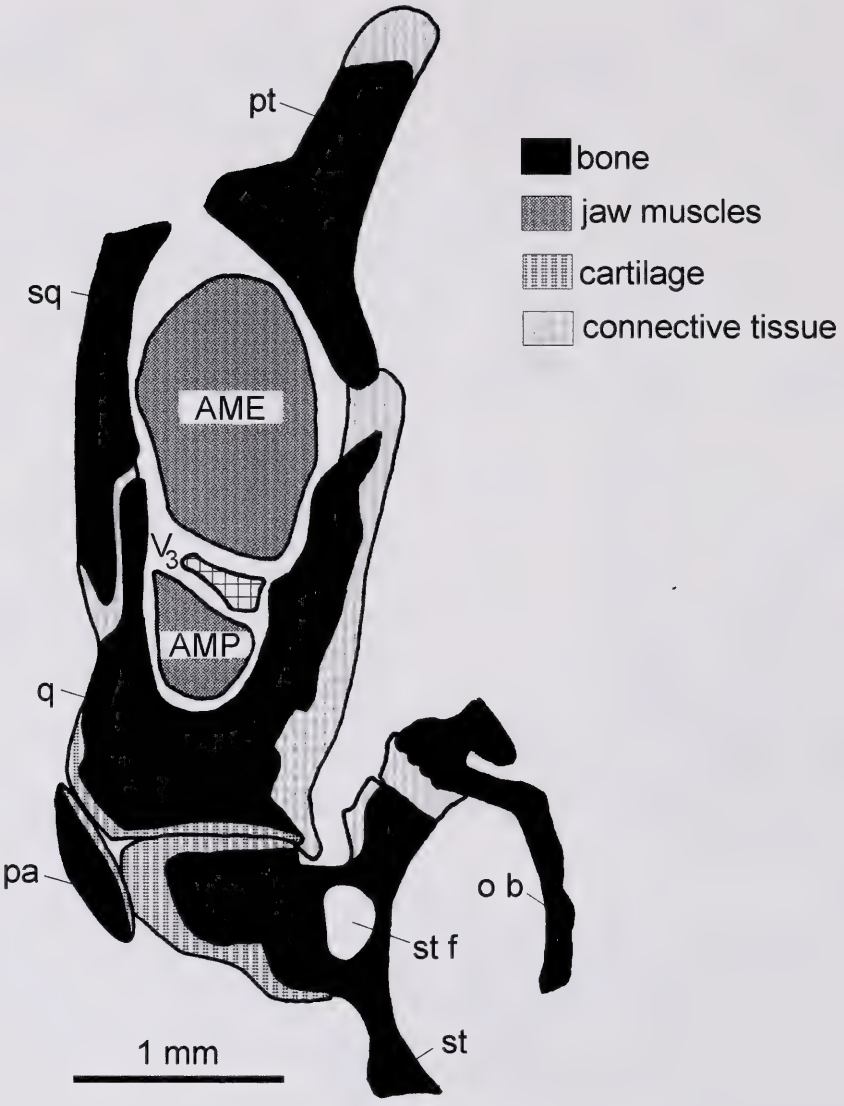

Figure 23. Horizontal section of the quadrate region of *Ichthyophis glutinosus* exhibiting an extensive cartilaginous contact between the stapes and quadrate, with both bones contributing to the facet for the pseudoangular. Based on serial sections in the collection of Marvalee H. Wake, Department of Integrative Biology, University of California, Berkeley.

unexpected specialization. Second, postulating the loss of an arterial foramen from one element and its reappearance in another would require at least some corroborative evidence, of which there is none.

Lower Jaw. Among the most durable of skeletal elements, the lower jaws of *Eocaecilia micropodia* are represented in articulation with several skulls (Figs. 3, 11, 13), as well as by numerous isolated specimens (Figs. 24–26). In contrast, no bones could be recognized as belonging to the hyobranchial apparatus, a not unexpected finding because the hyobranchial apparatus does not ossify in the adults of Recent caecilians.

Eocaecilia micropodia shares with most living caecilians the following unique combination of mandibular features:

The jaw comprises two distinct bones—the pseudodentary and the pseudoangular—which extensively overlap along their medial and lateral surfaces, respectively, and are thus joined along a wide suture that transects the jaw obliquely (Fig. 25C, D). There is no trace of any other separate ossification. The pseudoangular, which incorporates the articular, forms the mandibular articulation with the skull (Figs. 24C, G, 25F, 26B).

A lingual (or splenial) row of pedicellate teeth, which parallels the primary labial

row, extends posteriorly from the symphysis to about the midpoint of the labial row (Figs. 24E, 26A). Data presented by Taylor (1968) demonstrate that the lingual row is a highly variable feature among gymnophionans. A row containing 2–20 teeth is present in representatives of three families (rhinatrematids, typhlonectids, and uraeotyphlids) but is altogether absent in scolecomorphids (*Scolecomorphus* spp., *Crotaphatrema bormuelleri*). Of the two genera of ichthyophiids, a lingual row is present in *Ichthyophis* but not developed in *Caudacaecilia*. Among caeciliids, many genera lack lingual teeth (*Boulengerula, Brasilotyphlus, Dermophis, Leutkenotyphlus, Microcaecilia, Mimosiphonops, Parvicaecilia, Pseudosiphonops, Siphonops*) but even more possess them (*Caecilia, Gegeneophis, Geotrypetes, Grandisonia, Gymnopis, Herpele, Hypogeophis, Idiocranium, Indotyphlus, Oscaecilia, Praslinia, Schistometopum, Sylvacaecilia*; for the last genus, see Wake, 1987a).

A well-defined mandibular fossa is developed on the dorsal surface of the pseudoangular for insertion of the adductor musculature (Figs. 24C, 27C). In the depths of the fossa is a foramen (Fig. 27C) whereby V_3 and accompanying vasculature are conveyed into an intramandibular canal. There is no adductor fenestra, as in anurans and salamanders.

The pseudoangular bears a robust internal process that projects dorsomedially (Figs. 24D, 25C, H). The apicobasal height and anteroposterior width (measured across its base) of the internal process is relatively greater, and in some cases substantially greater, than that found in a sample of extant gymnophionans (Table 1). The pseudoangular also bears an elongate, posteriorly projecting retroarticular process that in life likely extended just caudal to the level of the occiput (Figs. 1A, 25D, 26B, 27C). The robustly constructed retroarticular process is slightly less than 20% of the lower jaw length, and thus shorter than those measured from selected extant taxa, which range from 20 to 32% (Table 1). The posterior terminus in a number of specimens is obliquely truncated (Fig. 27D) so as to face posterolaterally, although this geometry is not seen in every specimen (e.g., Fig. 24C). A slightly raised area developed on the terminus extends onto the dorsal aspect of the process (Fig. 24A, C); the area appears to represent a muscle insertion, probably for the interhyoideus posterior. A rugose depression, on some specimens linear (Fig. 25B) but on others irregular (Fig. 24C, G), is situated on the dorsal aspect of the process and might represent the insertion of the depressor mandibulae.

The arrangement of neurovascular foramina is also similar to those in Recent taxa. In *Hypogeophis rostratus* (Lawson, 1963) and other living caecilians, the mandibular branch of cranial nerve V and the mandibular artery and vein pass into the lower jaw via a foramen in the floor of the adductor fossa. A comparable arrangement occurs in *Eocaecilia micropodia,* although two foramina, rather than one, are present (Fig. 24C, G). The neurovascular bundle is distributed to two regions. First, the intramandibular branches of the mandibular vasculature and the ramus intramandibularis of V exit about midway along the medial surface of the jaw through a conspicuous intramandibular foramen. A comparable foramen is present in *Eocaecilia micropodia* (Figs. 24D, 25C, 27B). Second, the external and alveolar branches of both the vasculature and nerve V continue through the ramus toward the symphysis. Small foramina on the medial and lateral surfaces of the symphysial region provide access to surrounding soft tissue; these are evident in *E. micropodia* (Figs. 24A, 27A, B). As in living forms, *E. micropodia* possesses a number of vascular foramina along the trough between the two tooth rows that served the spongy tissue surrounding the tooth rows.

In *Dermophis* and *Gymnopis,* the ramus alveolaris of cranial nerve VII enters the lower jaw through a foramen that lies posterior to the base of the internal process,

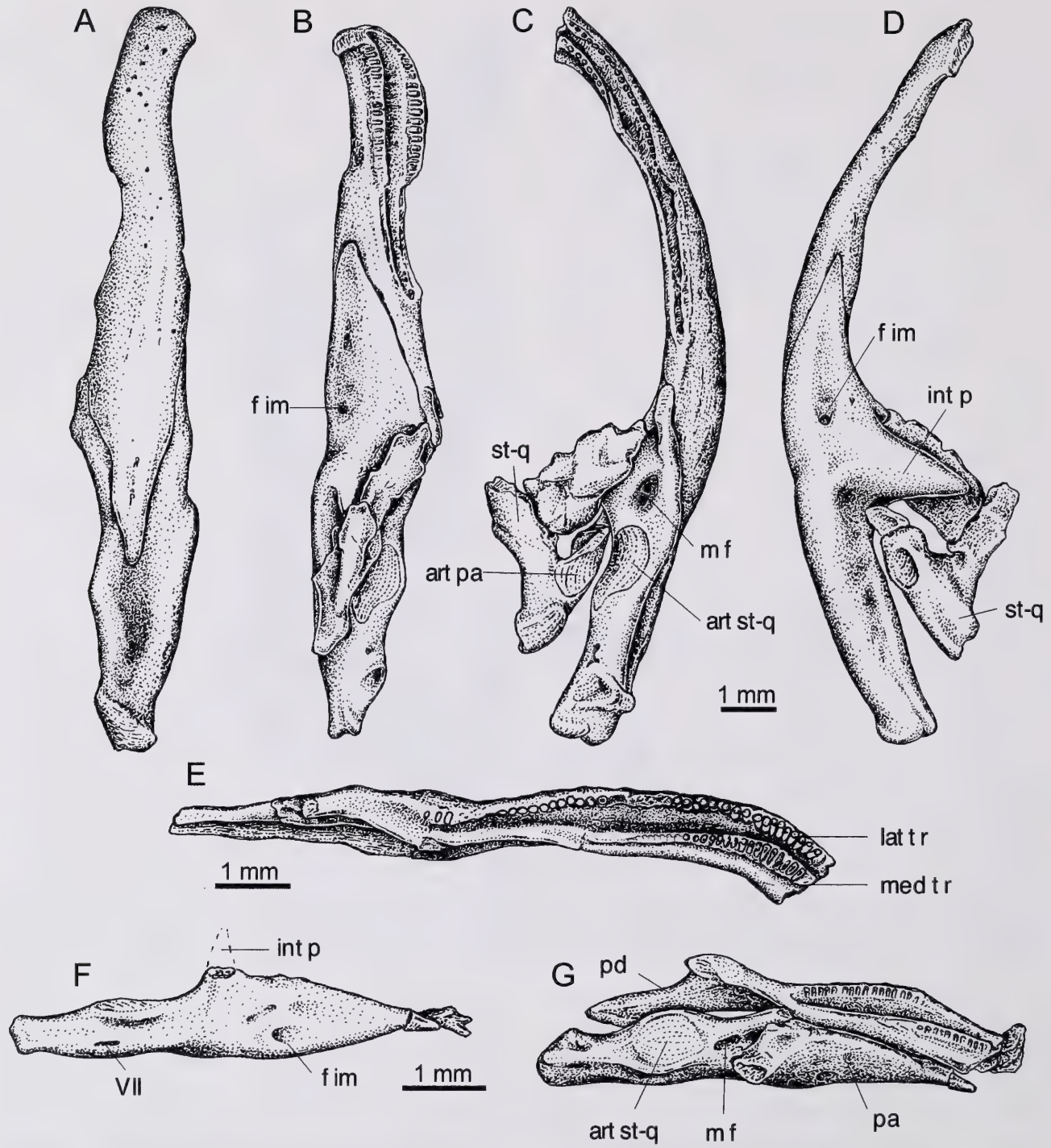

Figure 24. The lower jaws of *Eocaecilia micropodia.* MNA V8070 in (A) lateral, (B) medial, (C) dorsal (see also Fig. 26B), and (D) ventromedial views. In D the jaw is oriented in the plane of the internal process to show the length of the process. (E) A pseudodentary (MCZ 9152) in dorsal view; see also Fig. 26A. (F) A pseudoangular (MNA V8058) in medial view. (G) MNA V8058, a pseudoangular and partial pseudodentary (rostral end missing) in oblique dorsomedial view.

approximately in the transverse plane of the jaw joint (for an illustration of *Hypogeophis rostratus,* see Lawson, 1963, fig. 9a, b). In *Eocaecilia micropodia,* the foramen is comparably positioned relative to the jaw joint but is separated from the internal process which is relatively larger and located in a more rostral position (Figs. 3, 24F, 27A–C). The foramen variably occurs either on the ventral margin of the bone or slightly displaced onto either the medial or lateral surface. In modern

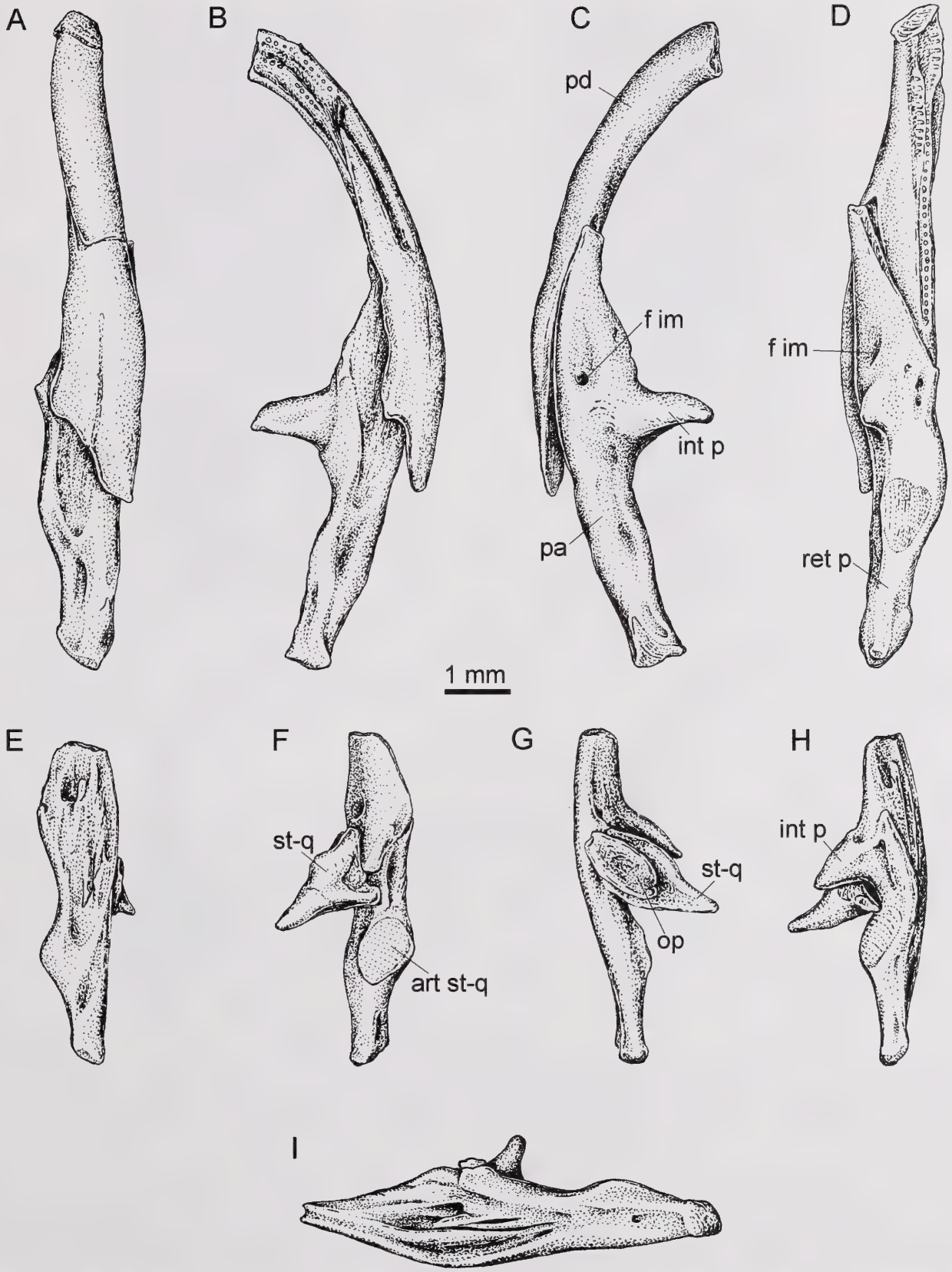

Figure 25. The lower jaws of *Eocaecilia micropodia*. MNA V8068 in (A) lateral, (B) dorsal, (C) ventral, and (D) medial views. MNA V8054, a pseudoangular in (E) medial, (F) dorsomedial, (G) ventral, and (H) dorsal views; the rostral end is oriented upward (as in A–D). (I) MCZ 9158, a pseudoangular in lateral view. (E, I) The extensive interdigitation at the pseudoangular-pseudodentary joint is shown.

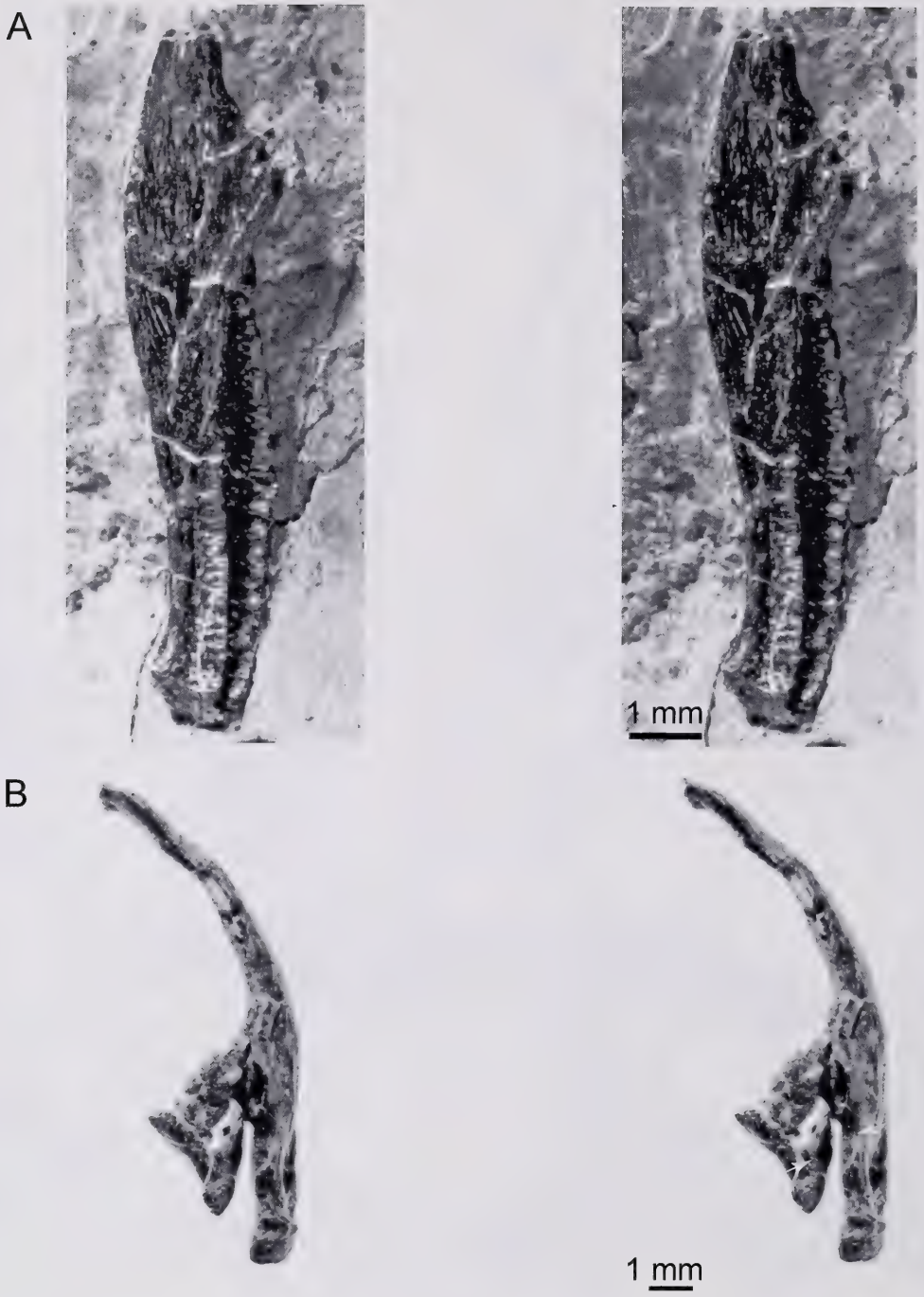

Figure 26. (A) A left pseudodentary of *Eocaecilia micropodia* (MCZ 9152) in medial view. (B) Right lower jaw and stapes-quadrate (MNA V8070) in dorsal view, showing the opposing articular facets of the stapes-quadrate and pseudoangular, here disarticulated and indicated by white arrows, comprising the jaw joint (stereophotographs); see also Fig. 24A–E.

caecilians, the ramus alveolaris of VII joins the ramus alveolaris of the V within the intramandibular canal where they run together toward the symphysis. The comparable arrangement of the intramandibular canal and foramen in *E. micropodia* and living caecilians would seem to indicate similarities in vascular and neural distribution. The intramandibular canal of *E. micropodia* was probably also occupied by a remnant of Meckel's cartilage, which is retained in Recent caecilians.

All of the foregoing characteristics of the lower jaw, considered together, indicate that the overall pattern of caecilian masticatory adaptations had been estab-

TABLE 1. RELATIVE SIZE OF THE INTERNAL AND RETROARTICULAR PROCESSES OF THE LOWER JAW IN *EOCAECILIA MICROPODIA* AND SELECTED TAXA OF EXTANT GYMNOPHIONANS. LENGTH OF THE RETROARTICULAR PROCESS (C) IS THE DISTANCE FROM THE POSTERIOR MARGIN OF THE ARTICULAR FACET TO THE POSTERIOR TERMINUS OF THE PROCESS. JAW LENGTH (D) WAS MEASURED FROM THE SYMPHYSIS TO A POINT MIDWAY BETWEEN THE RETROARTICULAR PROCESSES (I.E., IN A SAGITTAL PLANE)*.

	A Anteroposterior width of the internal process across the base (mm)	B Apicobasal height of the internal process (mm)	C Length of the retroarticular process (mm)	D Anteroposterior length of the jaw (mm)	A/D Relative width of internal process (%)	B/D Relative height of internal process (%)	C/D Relative length of the retroarticular process (%)
Eocaecilia micropodia MNA V8066	2	1.8	2.25	12.7	16	14	18
Eocaecilia micropodia MNA V8068	1.3	1.5	1.8	10.4	13	14	17
Epicrionops petersi USNM 160360†	0.7	1	4	13	5	8	31
Ichthyophis glandulosis MCZ 140003	1.2	0.7	2.6	12.7	9	6	20
Dermophis mexicanus MCZ 12121	1.4	2	4.7	18.4	8	11	26
Gegeneophis ramaswamii MCZ 29460	0.5	0.6	2.35	7.8	6	8	30
Gegneophis ramaswamii MCZ 29458	0.5	0.6	2.3	7.3	7	8	32
Gymnopis multiplicata MCZ 29265	1.3	1.1	5	18.4	7	6	27
Typhlonectes compressicauda MCZ 24524	2	1 e	5.1	20.5	9.8	5	25

* e, Estimated from a damaged specimen.
† Data from Nussbaum (1977, fig. 2).

lished by Early Jurassic times. No evidence appears of derived similarities with the jaws of frogs and salamanders, and yet in several features of mandibular morphology, notably the geometry of the jaw articulation, the large size and dorsomedial orientation of the internal process, and the large number and small size of the pedicellate teeth, *Eocaecilia micropodia* is distinctively different from any living gymnophionan.

The mandibular articular facet in *Eocaecilia micropodia* is set on the dorsomedial aspect of the pseudoangular, positioned posterior to the internal process and the mandibular fossa (Figs. 24C, G, 25D, 26B). The facet is oriented dorsomedially (Fig. 29A). In outline, the articular surface is irregularly oval, with the long axis of the ovoid passing from the facet's posterior, ventromedial margin to the anterior, dorsolateral margin. The surface of the facet exhibits a gentle concavoconvexity; the posterior, ventromedial half of the surface is slightly convex (MCZ 9158; MNA V8054, V8068, V8070), whereas the anterior, dorsolateral half is shallowly concave (MCZ 9158, MNA V8068) or more or less flat (MNA V8054, V8070). In MCZ 9235, the left pseudoangular and stapes-quadrate were preserved together but slightly disarticulated; preparation of the bones from the matrix permitted a comparison on the relative size of apposing facets as measured in planar view. The pseudoangular facet is larger, being 1.5 mm anteroposteriorly and 1 mm dorsoventrally. The analogous dimensions of the stapedial-quadrate facet are 1.1 and 0.8 mm, respectively. Pseudoangular facets preserved on other specimens give comparable anteroposterior and dorsoventral dimensions: 1.8, 1.3 mm (MNA V8070); 1.5, 1.1 mm

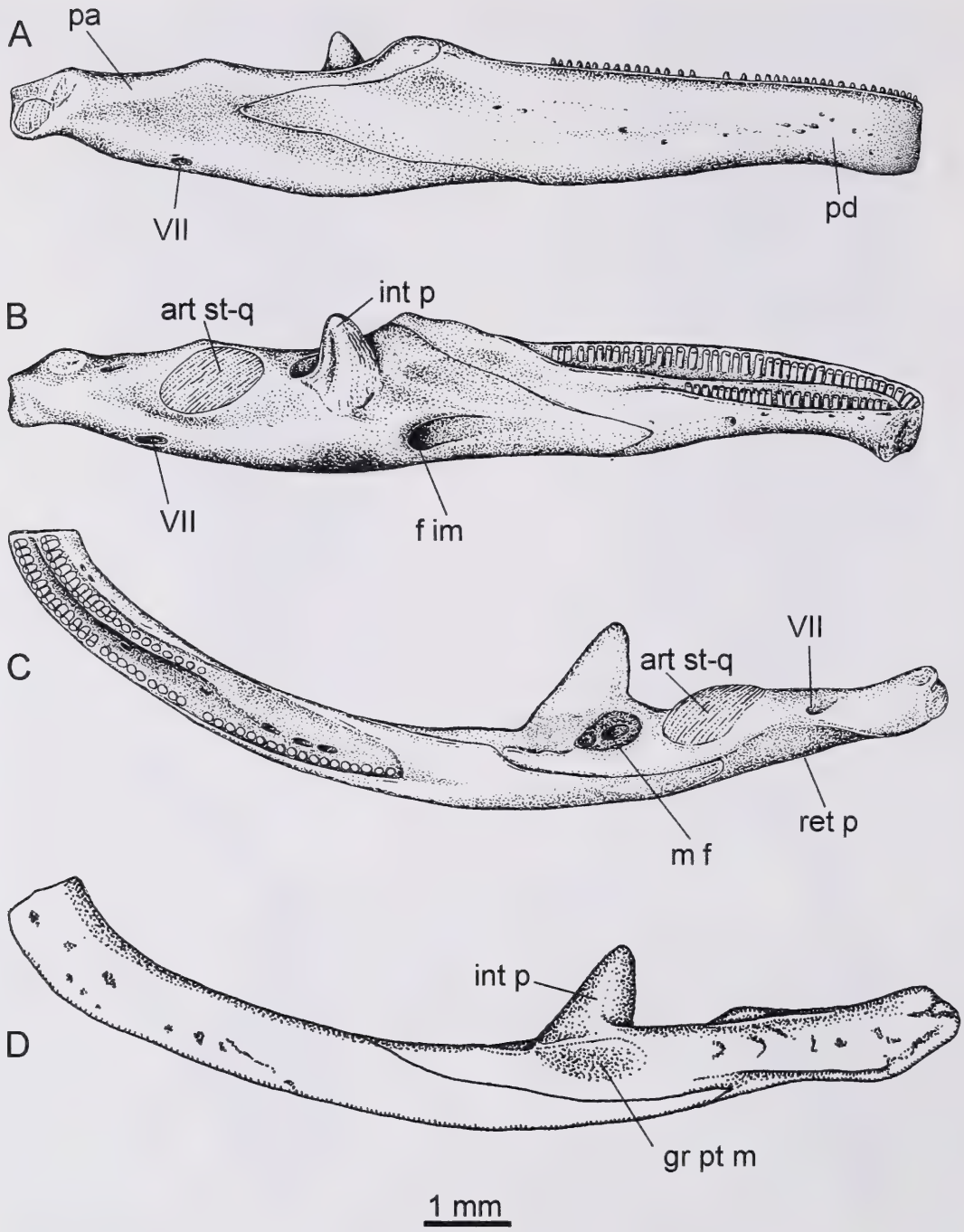

Figure 27. A reconstruction of the lower jaw of *Eocaecilia micropodia* based on the holotype (MNA V8066) and specimens illustrated in Figures 24–26. (A) Lateral, (B) medial, (C) dorsal, and (D) ventral views. The foramen for the ramus alveolaris of VII variably occurs on the lateral (A) and medial (B) aspects of the retroarticular process.

(MNA V8068); 1.4, 1.1 mm (MNA V8054); 1.25, 0.9 mm (MCZ 9158).

The pseudoangular facet would appear to correspond, in position and orientation, with the posterolateral half of the more extensive, U-shaped articular fossa (the processus condyloides of Nussbaum [1977, fig. 2]) that is characteristic of gymnophionans (Fig. 29B, C) and is also present in the Early Cretaceous caecilian *Rubricacaecilia monbaroni* (Evans and Sigogneau-Russell, 2001, fig. 3). However, the posterolateral component of the mandibular facet in Recent caecilians is not only more vertically inclined and more laterally placed than the facet in *E. micropodia*, but faces primarily anteromedially (rather than dorsomedially, as in *E. micropodia*). The

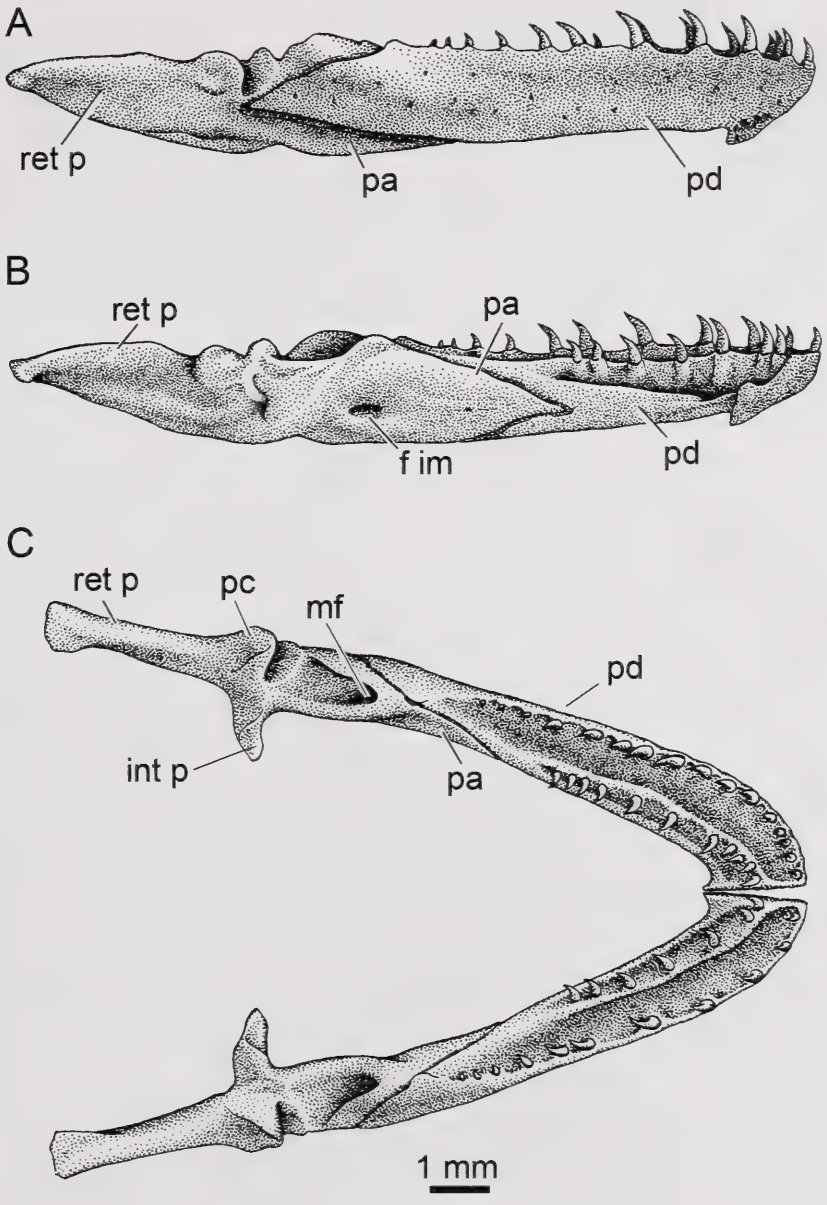

Figure 28. The lower jaw of *Epicrionops petersi* (from Nussbaum, 1977, fig. 2) in (A) lateral, (B) medial, and (C) dorsal views.

primary difference between the configuration of the mandibular facets of modern caecilians and *E. micropodia* is that, in the former, an anteromedial component of the facet is recurved to form a U-shaped fossa, whereas the entire facet in *E. micropodia* is, by comparison, essentially planar.

The internal process of *Eocaecilia micropodia* is notable for its large size. Relative to the length of the lower jaw, the process has greater apicobasal height, as well as greater anteroposterior width across the base, than those in selected representatives of Rhinatrematidae, Ichthyophiidae, Caeciliidae, and Typhlonectidae (Table 1). Only scolecomorphids lack an internal process (Nussbaum, 1985). Furthermore, the process in *Eocaecilia* differs in position, lying approximately at the level of the mandibular fossa for adductor musculature and anterior to the jaw articulation, whereas in Recent taxa, the base of the internal process is typically at the level of the jaw articulation and slightly posterior to the adductor fossa. In all of these features, *E. micropodia* also differs from the Early Cretaceous caecilian *Rubricacaecilia monbaroni,* which Evans and Sig-

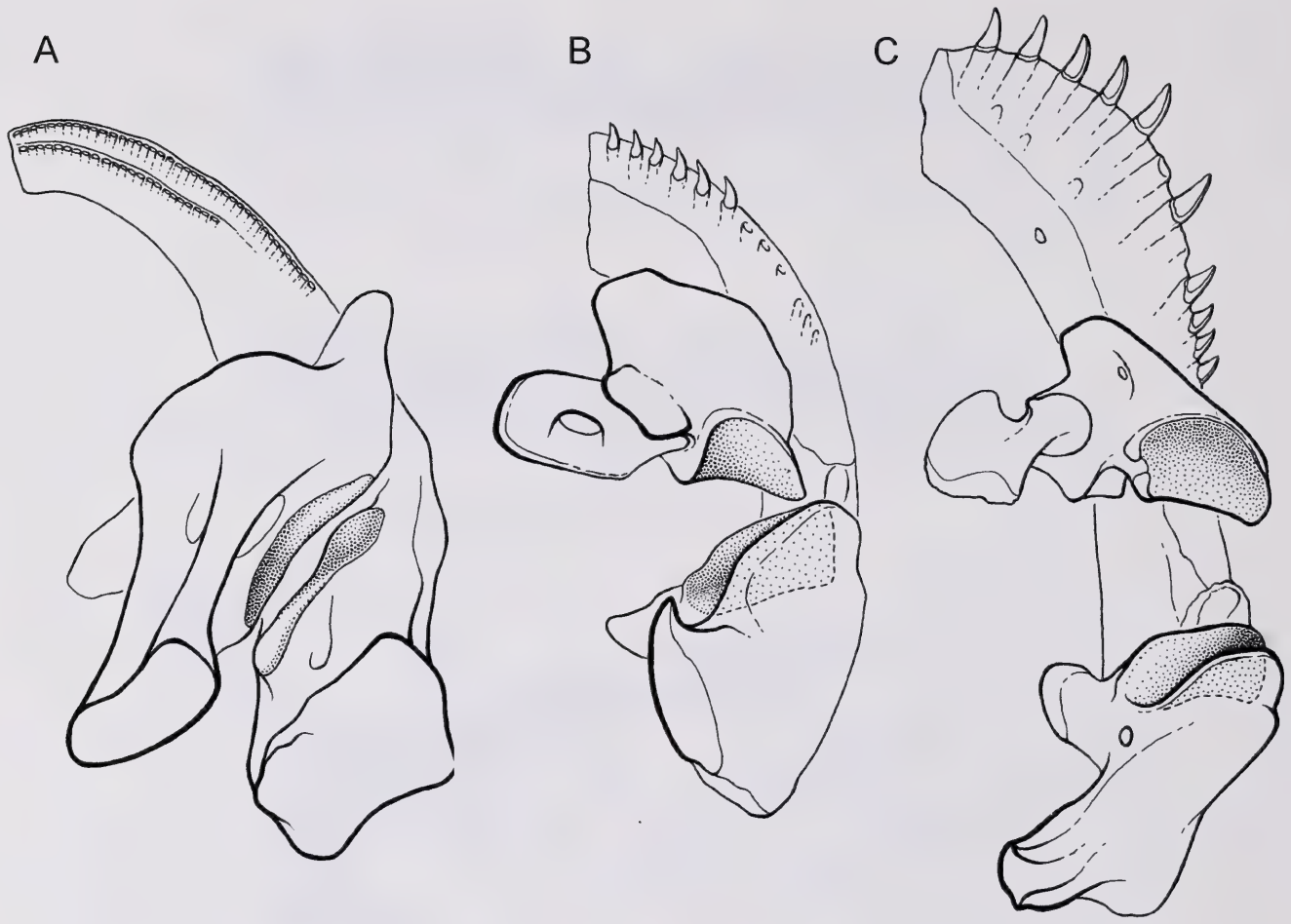

Figure 29. Posterodorsal views of the jaw joints of (A) *Eocaecilia micropodia* (reconstructed primarily from MCZ 9152), (B) *Ichthyophis glandulosus* (MCZ 14003), and (C) *Dermophis mexicanus* (MCZ 12121). In each case, the articular surfaces have been separated to show the geometry of the facets. Not to scale.

ogneau-Russell (2001: 267) noted most closely resembles the condition of rhinatrematids.

In Recent taxa, the relatively short internal process lies below the adductor chamber of the skull and is directed medially, whereas in *E. micropodia,* the elongate internal process must have projected dorsomedially into the adductor chamber, with its distal end extending above the horizontal plane of the quadrate ramus of the pterygoid. The dorsomedial inclination of the internal process is evident in several specimens (Figs. 4B, 13B, C, 25I). The degree of vertical inclination was probably sufficient to ensure that the process did not overlie the quadrate ramus of the pterygoid when the mouth was closed (constraining mouth gape) and thus could be withdrawn from the adductor fossa when the mouth opened. Nonetheless, the proximity of the process to the pterygoid is clearly evidenced by specimens in which the jaws are preserved in articulation with the skull. Typically the pterygoid is broken by compaction across the internal process, an artifact most clearly seen in the type (Fig. 3) and MCZ 9015 (Fig. 13B).

The pseudodentary bears two rows of teeth, as in rhinatrematids, typhlonectids, uraeotyphilds, *Ichthyophis,* and various caeciliids. The pseudodentary teeth of *Eocaecilia micropodia,* all of which are pedicellate, are more numerous than those in almost any modern caecilian, with the exception of *Praslinia cooperi.* In most specimens, the pedicels are closely packed, with a few gaps representing an unoccupied tooth locus or loci. As in most specimens of the upper jaw, no lower jaw

crowns are preserved in place, but the diameter of the pedicels is comparable. A sample of 15 well-preserved pedicel bases drawn from MCZ 9152, MNA V8058, and MNA V8068 range in diameter from 0.9 to 0.14 mm, with a mean of 0.11 mm. MCZ 9233 documents a slight size disparity between marginal row pedicels (mean diameter 0.13 mm, $N = 5$) and those of the inner row (mean diameter 0.09 mm, $N = 8$). The left jaw of MCZ 9235, although fractured in two places, possesses 37 pedicels in the marginal row, but if tooth positions are counted where pedicels appear to have been lost, the tooth count is 46; the inner row is not preserved. Contrary to the common practice among caecilian workers, we attempt to count or estimate the total number of tooth positions, although we distinguish between those that are confirmed on the basis of existing pedicels and those estimated from the length of a gap in the dental row. Given the nature of the fossil material, we cannot distinguish between loci which were actually unoccupied and those loci from which a pedicel and tooth crown were lost postmortem. Wake's (1976, 1980b) studies of caecilian dental development demonstrated that not all tooth loci are occupied through successive generations of teeth, but given the nature of the preservation of *E. micropodia*, we can only focus our account on the evidence for the total number of loci.

The jaw that most completely preserves both dental rows (MCZ 9152, Figs. 24E, 26A) has a marginal row bearing at least 40 and possibly as many as 43 tooth positions; 36 pedicels are present, with 4 or more lost postmortem, leaving short gaps in an otherwise continuous tooth row. The lingual (or splenial) row comprises an estimated 22 or 23 positions; only 16 pedicels are preserved in the lingual row, although distally there are vertical grooves in the pseudodentary that are evidence of some 6 or 7 pedicels lost postmortem. The two tooth rows are separated by a deep groove, and another groove is medial to the lingual row. The spacing between the two mandibular rows appears to be narrower than that between the premaxillary–maxillary and vomer–palatine rows. In the best preserved mandibular tooth rows (MCZ 9152, Fig. 26A), the lingual side of the marginal row is separated by 0.25 mm from the labial side of the lingual row; this distance, which was measured at the distal end of the lingual row, narrows further in the symphyseal region. In no skull, however, are the marginal and lingual rows sufficiently exposed and well preserved to permit an accurate measurement of their separation; a rough estimate of 0.6–0.7 mm can be made from MNA V8059 (Fig. 7). Our interpretation is that, with the jaws closed, the two mandibular tooth rows would have been positioned between the upper tooth rows (as is the case in the holotype skull; Fig. 4B).

Comparative Dental Morphology and Tooth Counts. Although tooth crowns are rarely preserved in situ on the pedicels, disarticulated tooth crowns were recovered by micropreparational techniques from several specimens (MCZ 9011, 9015, 9169), either immediately adjacent to the bases of pedicels or in close association with a skull. The crowns, which are conical, bicuspate, and recurved (Fig. 30; Jenkins and Walsh, 1993, fig. 1c, d), resemble those in some Recent gymnophionans (e.g., *Ichthyophis glutinosus, Uraeotyphlus narayani, Hypogeophis rostratus, Geotrypetes seraphini,* cf. Wake and Wurst, 1979, figs. 12–19). However, the teeth are minute in comparison with those of most living caecilians of comparable skull size and could only be examined in detail by scanning electron microscopy (SEM). Ten tooth crowns were successfully extracted from the matrix for this purpose, mounted on SEM discs, and provide a basis for assessing variation in size and structure.

Apicobasal crown heights in this sample range from 0.16 to 0.26 mm, with a mean and standard deviation of 0.22 and 0.03 mm, respectively. The mesiodistal breadths of crown bases (measured from

the labial aspect of the tooth, e.g., Fig. 30A) range from 0.09 to 0.13 mm (mean 0.11 mm, SD 0.012). The labiolingual breadths range from 0.08 to 0.14 mm (mean 0.12, SD 0.15). In seven of the 10 crowns, the bases are oval; in six crowns, the linguolabial diameter exceeds the mesiodistal diameter by 8–20%, whereas in one crown, the mesiodistal diameter is 11% longer than the linguolabial. In three specimens, the bases are circular. The small sample also displays a modest amount of variability in the shape of cusps and the lengths of crests. The crests on the apical cusp (or lingual cusp of Wake and Wurst, 1979) can be symmetrically lanceolate (Fig. 30A) or exhibit various degrees of asymmetry that arise from differences in the curvatures of the crests descending from the apical cusp (Fig. 30D, G, I) or in the inclination of the cusp as a whole (cf. Fig. 30A, G). Similarly, the secondary cusp (or labial cusp of Wake and Wurst, 1979) can be asymmetrical or symmetrical in terms of the lengths of the crests (cf. Fig. 30A, D). Although the primary cusp is always inclined lingually, the degree of inclination varies (cf. Fig. 30C, L).

Wilkinson (1991) described variations in the monocuspid tooth crowns of adult typhlonectids that appear to be in part comparable to those observed in the bicuspid teeth of *Eocaecilia micropodia,* despite the fact that the two taxa differ substantially in overall crown structure. In typhlonectids, the mesial and distal flanges descending from the single cusp are symmetrical on anterior teeth, but on posterior teeth, the mesial flange is relatively reduced and, on the posteriormost teeth, could be essentially absent. Wilkinson (1991: 305) also noted that "the curvature of teeth in more posterior loci tends to be skewed, such that these teeth project more posteriorly than they would if their curvature were restricted to a plane perpendicular to the tooth series." Symmetries and asymmetries of crest development, and skewing of the curvature, are evident in *E. micropodia* (Fig. 30). The dental morphology and arrangement of fetal *Typhlonectes compressicaudatus* differ substantially from those of adults (Hraoui-Bloquet and Exbrayat, 1996); the tooth crowns of *E. micropodia,* despite their very small size, are associated with adult specimens with comparably small pedicels and thus appear not to represent an ontogenetically immature stage.

From a study of complete dentitions in two specimens of *Gegeneophis ramaswamii,* Greven (1984) documented considerable variation in the degree of development of the secondary cusps on upper teeth and found that lower teeth were monocuspid. We have no evidence that tooth crown variability in *E. micropodia* attained comparable heterogeneity.

The observation that the conical, bicuspate, recurved teeth of *Eocaecilia micropodia* exhibit only modest variability parallels the conclusion reached by Wake and Wurst (1979: 332) from their morphological study of teeth of selected specimens from four families: Ichthyophiidae, Uraeotyphlidae, Caeciliidae, and Typhlonectidae. In contrast to the marked structural diversity noted by these authors across species, they reported "little variation within species . . . although size of crown and curvature vary slightly with ages and sizes of specimens . . . with larger, more recurved teeth found anteriorly on the jaws, particularly the dentaries . . . teeth are replaced on the jaws throughout the lives of the animals [and] those at particular loci are larger with each replacement."

The number of teeth in *Eocaecilia micropodia* (44–51 in the premaxilla–maxillary row, about 34 in the vomeropalatine, and 40–43 and 22 or 23 in the labial and lingual pseudodentary rows, respectively) is greater than in any known living caecilian, with a single exception. The estimated tooth count in *E. micropodia* is, by necessity, a composite based on the best evidence from multiple specimens and provides no account of the variability that commonly occurs among living caecilians,

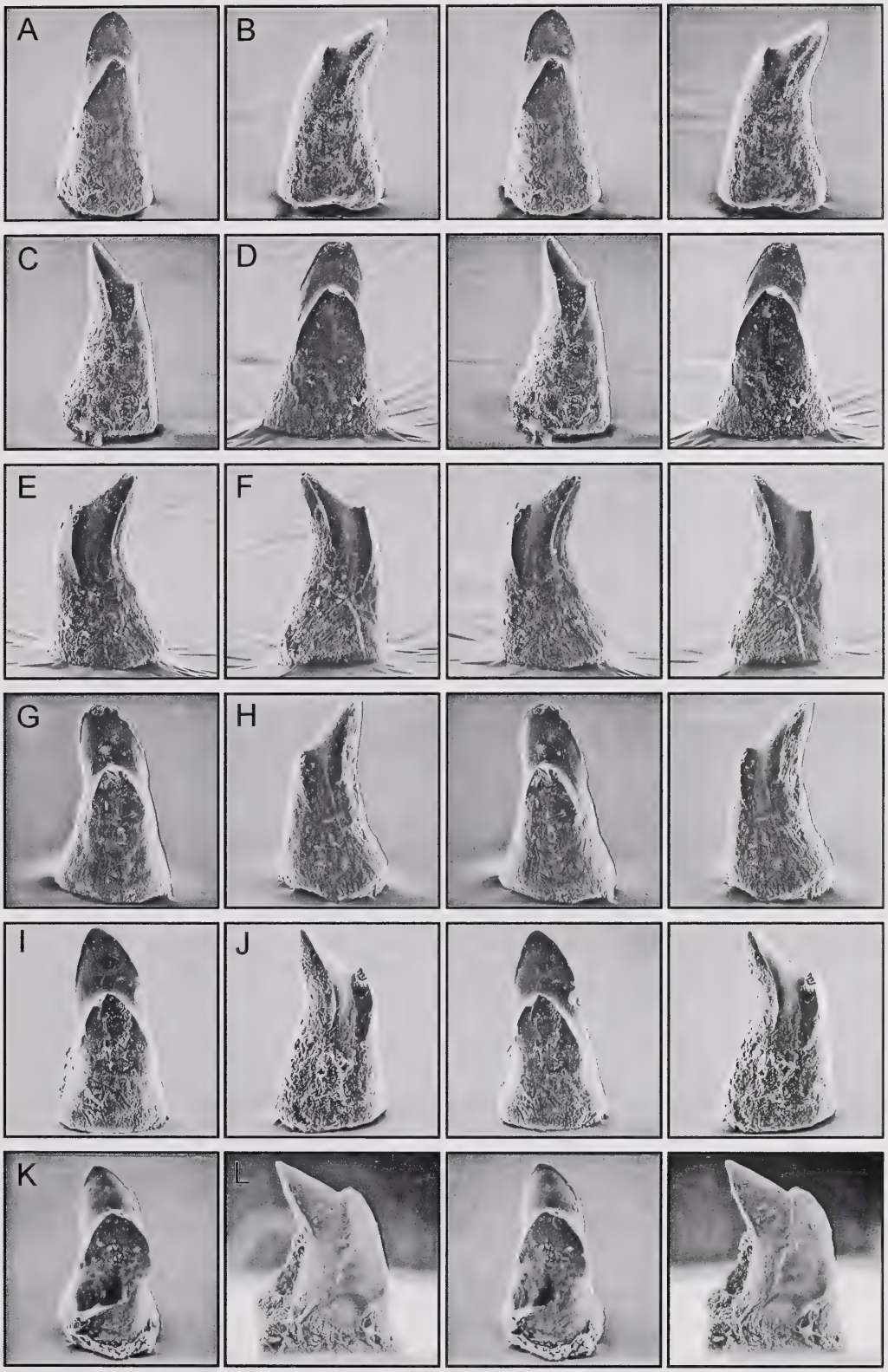

Figure 30. Stereophotographic scanning electron micrographs of tooth crowns of *Eocaecilia micropodia.* Lingual and labial surfaces are identifiable on the basis of crown curvature and relative size of the cusps. The relative tooth positions represented by these isolated crowns cannot be determined, and therefore side views are designated "mesiodistal," with no certainty that the view is anterior (mesial) or posterior (distal). (A) MCZ 9011 in labial view, (B, C) opposite views along the mesiodistal axis; the apicobasal height of the tooth is 0.25 mm. (D–J) Three teeth from MCZ 9169. (D) Labial view and (E, F) opposite views along the mesiodistal axis; the apicobasal height is 0.20 mm. (G) Labial and (H) mesiodistal views; the apicobasal height is 0.24 mm. (I) Labial and (J) mesiodistal views; the apicobasal height is 0.25 mm. MCZ 9015: (K) labial and (L) mesiodistal views; the apicobasal height is 0.16 mm.

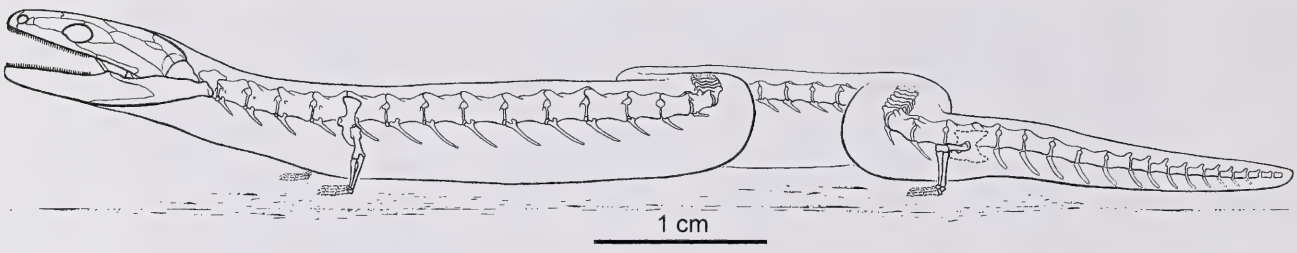

Figure 31. A composite reconstruction of *Eocaecilia micropodia* depicting the relative size of skull, vertebrae, limb girdles and limbs.

where tooth number increases with body size and age. Nonetheless, these uncertainties do not eclipse the fact that *E. micropodia* possesses about twice the number of teeth as most gymnophionans. In a survey of 158 Recent taxa, Taylor (1968) reported 99 species (or 63%) with unilateral tooth counts of 20 or fewer in the premaxilla–maxillary, vomeropalatine, and pseudodentary rows; 136 species (or 86%) have 25 or fewer. At the upper end of the range are the ichthyophiids *Ichthyophis elongatus* and *Caudacaecilia nigroflava*, both with about 30 teeth in the premaxilla–maxillary, vomeropalatine, and pseudodentary rows (Taylor, 1968).

In his original description of the Seychellean species *Praslinia cooperi*, Boulenger (1909: 292–293) noted that "... the teeth are more numerous than in any other known genus of Caeciliids ... [with] 40 to 48 teeth on each side of the upper jaw, and about as many in the outer mandibular series on each side; about 45 inner mandibular teeth altogether." Close examination of Boulenger's illustration (1909, fig. 1b) shows a unilateral count of 47 premaxilla–maxillary teeth, 40 vomeropalatine teeth, and 47 or 48 and 25 or 26 in the labial and lingual pseudodentary rows, respectively. Subsequent authors report comparably high counts; Parker (1941) cited 36–48 premaxilla–maxillary teeth, and Nussbaum and Wilkinson's (1989: 37) diagnosis of this monotypic genus includes "teeth small, uniform in size, more than 50 per row, except for the splenials." No data on the diameter and height are available in the literature; measurements made with an ocular micrometer of the teeth illustrated by Boulenger (1909, fig. 1b) yield a tenuous estimate of an apicobasal height of 0.17 mm, which is in the range observed for *Eocaecilia micropodia* teeth. Thus *P. cooperi* is the only known living caecilian with teeth in equivalent numbers and size as those in *E. micropodia*, and it is therefore regrettable that little is known of the dietary habits of this species; Nussbaum (1984) was unsuccessful in his earlier attempts to collect this apparently rare caecilian but has since reported (personal communication) collecting several specimens.

The Cretaceous caecilian *Rubricacaecilia monbaroni* appears to have had fewer teeth in the lower jaw than *Eocaecilia micropodia*—with 28 in the labial pseudodentary row and only two in the lingual (splenial) row (Evans and Sigogneau-Russell, 2001). Yet, like *E. micropodia*, the teeth of *R. monbaroni* are very small, with a basal diameter of about 0.3 mm (estimated from Evans and Sigogneau-Russell, 2001, fig. 4B). Although the base of the crowns are thus about twice that of *E. micropodia*, both fossil taxa have, by comparison to those of most living caecilians, diminutive dentitions.

Postcranial Skeleton

Overview. Postcranial bones are abundant among the available materials of *Eocaecilia micropodia*; most elements, with the exception of the pelvis, manus, and pes, are represented by multiple specimens. The relative completeness of this assemblage provides a sound basis for a reconstruction that depicts the relative size of the skull, vertebrae, and limbs (Fig. 31).

Although the number of vertebrae cannot be precisely determined on the basis of available material, there is sufficient evidence from several specimens, reviewed below, that the presacral region of *E. micropodia* was elongate, as in modern caecilians. A distinct tail was present, comparable to the postcloacal region of rhinatrematids, ichthyophiids, and uraeotyphlids (Nussbaum, 1977; Nussbaum and Wilkinson, 1989). Relative to the size of the vertebrae, the limb bones and girdles are diminutive.

Postcranial Axial Skeleton

In Recent caecilians, the vertebral column can be most simply described as being composed of an atlas, a large number of trunk vertebrae, and, in taxa in which postcloacal vertebrae occur, caudal vertebrae. The subtly gradational nature of the axial column poses a challenge to distinguishing vertebral regions. In a study of *Hypogeophis rostratus,* Lawson (1963: 271) concluded that "with the exception of the first or atlas . . . , [the vertebrae] are essentially of a uniform structure without regional variation." In contrast, Wake (1980a) identified regional differences in both structure and growth allometry in *Dermophis mexicanus, Ichthyophis glutinosus,* and *Typhlonectes compressicauda* that characterize "cervical," midbody, and posterior vertebrae. Although Taylor (1977) initially suggested that modifications of the anterior four or five vertebrae were sufficiently distinctive to designate them cervicals, Wake (1980a) demonstrated on the basis of the taxa included in her study that the number of distinctive anterior vertebrae is much larger. The first 20 vertebrae typically possess a longitudinal nuchal keel; short, widespread parapophyses; and broad, relatively flat pre- and postzygapophyses; Wake suggested that these "cervical" features are related to stabilizing and elevating the head during burrowing.

Comparison of vertebral regions in *Eocaecilia micropodia* with those of modern caecilians cannot be undertaken with certainty throughout the axial skeleton because no specimen preserves a complete vertebral column. Nonetheless, the atlas is well known, and the identity of the second vertebra (axis) and other vertebrae associated closely with the atlas is secure; these are referred to as postatlantal (PA) vertebrae, rather than cervical (C), for they largely lack those features that characterize the "cervicals" of living caecilians (fide Wake, 1980a). If the precise location of the shoulder girdle along the postatlantal vertebral column were known, a cervical region might be securely identified. The shoulder girdle and forelimb elements in MCZ 9169 (Fig. 35) are disarticulated and not certainly in place with respect to the associated vertebral column. Lacking evidence in any specimen of enlarged ribs on postatlantal vertebrae, which might also indicate the placement of the shoulder girdle, the length of the "cervical" region remains moot. A sacral region is known, as is the caudal series. The fact that the analysis and description of the vertebral column is based on several incomplete specimens removes the possibility of using within-column variations in size as a useful descriptor.

Wake (1970: 33) expressed the opinion that "without fossil evidence, identification of the centrum of modern amphibians [frogs, salamanders, and caecilians] with the pleurocentrum of fossil forms is not warranted." *Eocaecilia micropodia* provides the desired evidence, for caecilians at least, by possessing small, crescentic intercentra. The gymnophione centrum thus appears to represent a pleurocentrum. Intercentra occur in specimens in which the atlas, axis, and other vertebrae of the postatlantal region are preserved in articulation. Intercentra also occur in a specimen interpreted as representing the anterior dorsal region. The absence of intercentra in other series of vertebrae could possibly reflect regional variation, but postmortem loss cannot be ruled out.

Atlas. The atlas, represented in several

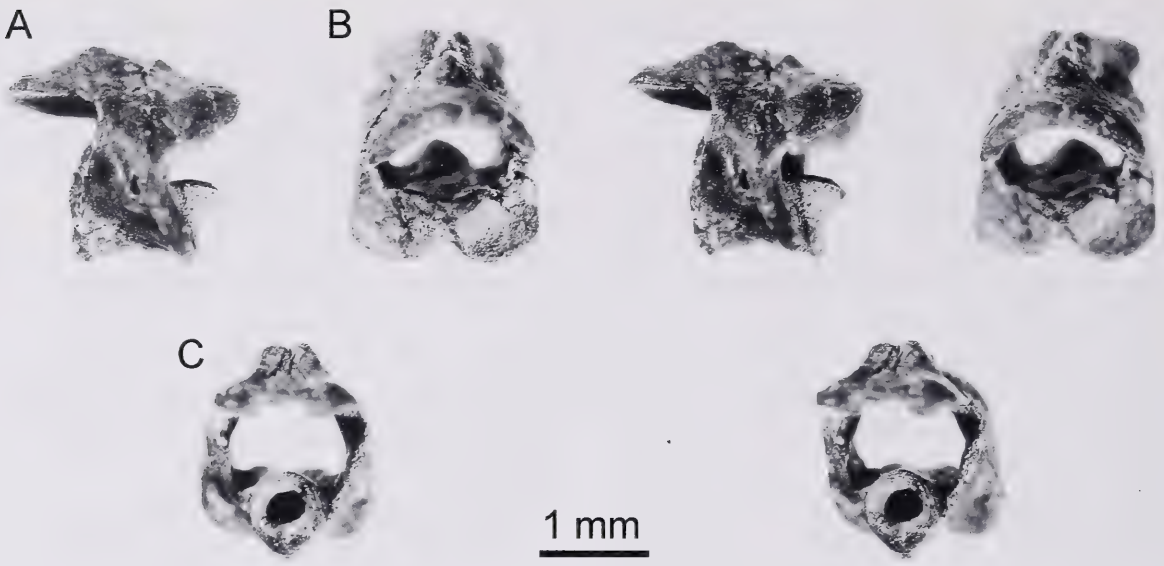

Figure 32. The atlas of *Eocaecilia micropodia* (MCZ 9231) in (A) lateral, (B) anterior, and (C) posterior views (stereophotographs).

specimens (MCZ 9167, 1969, 9171; MNA V8059, V8066), is best preserved in MCZ 9231 (Fig. 32), which serves as the primary basis for the following description. The length of the atlas centrum, excluding the pyramidal interglenoid tubercle that prolongs the floor of the neural canal rostrad (Fig. 32A), is 1.5 mm. An interglenoid tubercle, a feature found in salamanders (Francis, 1934), certain microsaurs (Carroll and Gaskill, 1978, figs. 115, 116), and albanerpetontids (McGowan, 1998), is not known to be present in any Recent gymnophionan (Wake, 1970). The two condylar facets (or cotyles) extend from the ventrolateral aspects of the interglenoid tubercle to the lateral margin of the centrum. The dorsomedial part of each condylar facet thus faces ventrolaterally and the lateral part rostrad (Fig. 32B). The anterior width of the centrum measured across the facets is 1.8 mm. On the ventral surface of the centrum is a distinct notch between the condylar facets; a rounded, median keel occupies the posterior ventral half of the centrum. A small, presumably vascular foramen occurs on the lateral side of the centrum. The posterior end of the centrum (Fig. 32C), excavated by a deep notochordal fossa, is 0.8 mm wide and 0.85 mm high.

No evidence exists of a diapophysis. MCZ 9169 (Fig. 33A) reveals that the head of the first rib articulated with the

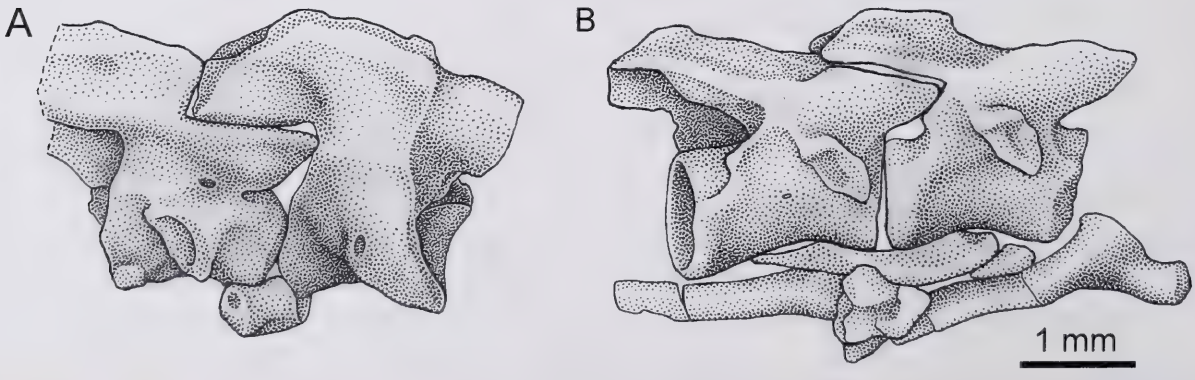

Figure 33. Vertebrae of *Eocaecilia micropodia* (MCZ 9169). (A) An articulated atlas and axis in lateral view. (B) Articulated vertebrae interpreted to be the sixth and seventh vertebrae of the vertebral column, lateral view.

atlantoaxial intercentrum and that the tuberculum articulated with the axial diapophysis. A foramen on the lateral surface of the base of each pedicle is a feature that is also present in other postatlantal vertebrae of *Eocaecilia micropodia.* A comparably situated intravertebral foramen, which communicates with the neural canal, occurs in the atlas in at least some Recent taxa: *Gymnopis multiplicata* (MCZ 29265) and *Dermophis mexicanus, Ichthyophis glutinosus,* and *Typhlonectes compressicauda* (Wake, 1980a). A foramen on the medial wall of the pedicle of the atlas and the following four postatlantal vertebrae in the holotype of *E. micropodia* (MNA V8066, Fig. 34) is evidence of a complete passage through the pedicle; therefore, the canal is most likely an intravertebral foramen for neuronal egress (rather than a vascular channel into the bone). Anteriorly the laminae (i.e., the dorsal roof of the neural arch) extend as an archlike prolongation over the interglenoid tubercle and probably closely approached the margin of the foramen magnum. The anteroposterior length of the arch from the anterior margin of the laminae to the tips of the postzygapophyses is 2.3 mm, or 0.8 mm longer than the length of the centrum. The postzygapophyses, rather than being distinct processes, are united across the midline by a thin lamina of bone. The orientation of the postzygapophysial facets is nearly horizontal; they face only slightly laterally. The central floor of the neural canal is relatively flat, but the laminae composing the roof are distinctly arched; the neural canal is thus hemitubular, in contrast to the condition typical of Recent caecilians in which the neural canal is tubular in cross section (for additional details of the atlantal neural canal, see the description of MNA V8066 below). The atlantal spinous process is represented only by a low tubercle; the spinous process appears to bifurcate posteriorly into a pair of faint ridges that extend posterolaterally onto the postzygapophyses.

The atlas of *Eocaecilia micropodia* resembles the incomplete atlas of *Rubricacaecilia monbaroni* from the Early Cretaceous in the presence of an interglenoid tubercle, the transverse orientation of the condylar facets, and the placement of a conspicuous neural foramen at the base of the pedicle (cf. Fig. 32; Evans and Sigogneau-Russell, 2001, figs. 4, 5A–C). Evans and Sigogneau-Russell (2001: 268, fig. 5A) interpreted the articular surfaces of the condyles in *R. monbaroni* as extending across the midline, implying an unusual condition in which the occipital condyles would be spaced very closely together. In *E. micropodia,* the facets are narrowly separated dorsally, but more widely separated ventrally by a distinct notch (Fig. 32B).

Vertebral Regions. Vertebrae and ribs are associated with many specimens of *Eocaecilia micropodia,* but relatively few are articulated in series (MCZ 9169; MNA V8055, V8062). Although no specimen preserves a complete presacral column, there is sufficient evidence from associated elements (the atlas, pectoral girdle and forelimb, and hindlimb) that five vertebral regions are identifiable: postatlantal, dorsal (including possibly middorsal), posterior dorsal, sacral, and caudal. With the exception of the caudal series, regional variations in structure are subtle.

Postatlantal Region. The holotype of *Eocaecilia micropodia* (MNA V8066, Fig. 34) preserves as an associated series the atlas, axis, and three additional postatlantal vertebrae (PA3–PA5). The vertebrae are damaged and slightly disarticulated postmortem; the left half of the neural arches are missing, probably as the result of the quarrying process. The length of the atlas centrum is 1.5 mm. Other centra are slightly longer; the axis and PA4 are 1.6 mm, and PA5 is 1.7 mm (the length of PA3, as preserved, is 1.5 mm, but this is probably an artifact). Overall vertebral lengths (measured from the rostral extremity of the prezygapophysis to the caudal extremity of the postzygapophysis) could only be estimated on PA2 and PA4 and are in the range of 2.2–2.3 mm.

Figure 34. (A) The holotype skull, atlas and associated postatlantal vertebrae of *Eocaecilia micropodia* (MNA V8066) at the completion of the initial stage of preparation and before removing the skull from the matrix. (B) Enlarged view of the vertebrae after detailed preparation; rostral is to the left. The loss of the left half of the neural arches exposes the right pedicles in medial view, which reveals an internal process on the medial surface of each pedicle (p i p, white arrows). Anteroventral to each process is the internal ostium of the intravertebral foramen (stereophotographs).

The loss of the left half of the neural arches of the atlas, axis (PA2), PA4, and PA5 (on PA3 the arch is completely broken away) exposes the internal surface of the neural canal. The medial openings of intravertebral foramina are evident on all pedicles. Bilaterally, along the pedicle–centrum junctions, the floor of the neural canal of the atlas is excavated by a deep, longitudinal sulcus. The rostral end of the sulcus begins at the transverse level of the medial opening of the intravertebral foramen; the sulcus extends caudally to the posterior end of the atlantal centrum. The two sulci together compose about two-thirds of the breadth of the neural canal;

in the midline, the floor of the neural canal is slightly convex, except in the region of the interglenoid tubercle where the surface is slightly concave. Comparable sulci are exhibited on the axis–PA5, although they differ by being transversely narrower and by extending the full length of the pedicle–centrum junction.

The most extraordinary feature of the neural canal is the presence of a bony process that projects medially from the internal surface of each pedicle (Fig. 34B). On the atlas, the process is situated directly posterior to the intravertebral foramen and near the pedicle–centrum junction; the atlas from another specimen shows the same feature (Fig. 15D). On the axis (PA2), the process is likewise posterior to the intravertebral foramen, but both the process and foramen are more dorsally positioned, approximately halfway up the internal face of the pedicle; the process, which is 0.2 mm in length, tapers to an apex and is directed medially and somewhat ventrally. The width of the neural canal of the axis is estimated to be 0.9 mm, but the two processes would reduce the space available for passage of the spinal cord to about 0.5 mm. On PA4 and PA5, the intravertebral foramina lie close to the pedicle–centrum junction, and the processes are situated posterodorsal to the foramina.

Internal processes within the neural canal of anterior vertebrae have not previously been reported in any Recent gymnophionan. A review of atlantal specimens in the MCZ Herpetology collection reveals that comparable processes do occur in some taxa but are apparently not common. Representatives of Ichthyophiidae (*Ichthyophis glandulosus,* MCZ 14003), Typhlonectidae (*Typhlonectes compressicauda,* MCZ 24524), and Scolecomorphidae (*Scolecomorphus kirkii,* MCZ 12234, 27120) exhibit pedicles with smooth internal surfaces. Similarly, a number of caeciliid species are without processes: *Boulengerula boulengeri* (MCZ 12309), *Dermophis mexicanus* (MCZ 12122), *Gegeneophis ramaswamii* (MCZ 29460), *Geotrypetes seraphini* (MCZ 3424), *Gymnopis multiplicata* (MCZ 29265), *Hypogeophis rostratus* (MCZ 48935), and *Oscaecilia ochrocephala* (MCZ 14817). In species of the caeciliid genus *Schistometopum,* however, processes are present. In *S. gregorii* (MCZ 20057, 20070) distinct digital processes are directed anteromedially, whereas in other specimens (MCZ 20055, 20146) the processes are less prominently developed and in some cases are low rugosities. Processes are also present in *S. thomensis* (MCZ 29450). In one specimen of *S. gregorii* (MCZ 20056), dry preservation of soft tissues reveals that the processes are anchor points for a connective tissue suspensory ligament (very likely the pia mater, as in the denticulate ligament) that passes to the ventral surface of the spinal cord. A specimen of the uraeotyphlid *Uraeotyphlus oxyurus* (MCZ 9484) bears low tubercles that are somewhat rugose.

Comparable structures occur in some snakes (e.g., boids, *Python,* Romer, 1956, fig. 129I; *Boa constrictor,* MCZ 13019; colubrids, *Coluber constrictor,* MCZ 160014; and elapids, *Ophiophagus hannah,* MCZ 67054) as a delicate, longitudinal ridge that runs anteroposteriorly along the medial aspect of the pedicle at a level comparable to that of the caecilian process. Illustrations of the atlas of a Cretaceous caecilian, *Rubricacaecilia monbaroni,* and the Recent form *Ichthyophis mindanaoensis* (Evans and Sigogneau-Russell, 2001, fig. 7B, E) might be interpreted to depict similar structures, but in neither case are the features comparable (S. E. Evans, personal communication).

MCZ 9169 preserves an atlas, axis (Fig. 33A), and at least four additional vertebrae in a more or less articulated series. The atlantal centrum is 1.3–1.4 mm in length, very slightly shorter than in MCZ 9231, but otherwise similar to the latter in almost all details, including the presence of both spinal and vascular foramina. The exception is the spinal region. In place of the single, median tuberosity observed in MCZ 9231, the spinous process is a very

narrow, low, elongate ridge (the nuchal keel of Recent gymnophionans; Wake, 1980a), flanked on either side by a small tuberosity.

The axial centrum of MCZ 9169, 1.6 mm in length, is separated from the atlas by an intercentrum that bears a posterolaterally directed parapophysis. Although the first rib is missing, the facet for the rib head is round and relatively large (0.4 mm diameter). The posteroventral margin of the axial centrum bears a raised parapophysial demifacet for the second rib (also missing). The axial diapophyses are more massive and project farther from the pedicle than any of the more caudal diapophyses; oval in cross section (diameters 0.7, 0.3 mm), the long axis is oriented obliquely (the caudal end is superior, the rostral end inferior). Above the diapophysis is a foramen, probably serving the same function as that in the atlas, but situated more dorsally on the pedicle. The spinous process, or nuchal keel, is a higher ridge than that on the atlas. A pair of tubercles, comparable to those that flank the spinous process anteriorly on the atlas, are posteriorly positioned on the dorsum of the postzygapophyses. The articulation between the atlas and axis confirms that the midline lamina of bone between the atlantal postzygapophyses intimately overlies the anterior part of the axial neural arch.

The third and fourth postatlantal vertebrae, disarticulated and somewhat displaced, are obscured by fractures and overlying bone fragments. Features that are evident (very low nuchal keel, bony lamina linking the postzygapophyses, orientation of the diapophyses) appear to be comparable to those of the axis. The centra, however, are longer (1.7–1.8 mm). An intercentrum is preserved along the anteroventral margin of PA3. A limb bone with a shaft diameter 0.4 mm and length of over 2 mm is associated with PA4; although the ends are somewhat crushed, the appearance most closely resembles a radius.

Proximal rib fragments associated with a skull (MCZ 9242, Fig. 12) are likely to be derived from the postatlantal region. The capituli and tuberculi, which are well separated, expand toward each terminus and bear a circular facet.

The postatlantal region, reconstructed from MNA V8066 and MCZ 9169, can only be distinguished on the basis of a single feature: spinal nerves traverse foramina through the pedicles on the atlas, axis, and at least the next three vertebrae, whereas on anterior dorsal vertebrae, the egress of spinal nerves appears to have been around the posterior margin of the pedicle. Otherwise, postatlantal vertebrae of MCZ 9169 are structurally gradational with those of the anterior dorsal region. Rostrocaudally, the length of centra increases from 1.4 mm on the atlas to 2.1 mm on the 11th vertebra, the angle of zygapophysial facets shifts from nearly horizontal to about 45°, diapophyses are reduced, and ribs become shorter and more slender, with more closely spaced capituli and tuberculi.

Anterior Dorsal Region. The next two vertebrae in the MCZ 9169 series are articulated and well preserved (Fig. 33B) and are separated from PA4 by a gap of approximately one vertebral length. Two lines of evidence support our interpretation that the gap represents a missing vertebra (or possibly vertebrae), and that the two next vertebrae are probably the sixth and seventh. First, the two vertebrae are lying on their left side, whereas PA4 is lying on its right side, indicating that the continuity of the series has been substantially disrupted. Second, the anterior vertebra of the pair is unlikely to represent PA5 because it lacks a spinal foramen in the pedicle, which is known to be present in PA5 of the holotype.

For purposes of the present description, the pair is designated as the sixth and seventh vertebra (Fig. 33B). The notochordal centra are 1.7–1.8 mm in length, with concave lateral and ventral surfaces. The pedicles are mounted anteriorly on the centrum. Both lack spinal foramina traversing

the pedicles. The posterior margins of the pedicles are deeply incised for passage of the spinal nerves; the intervertebral "foramen" is therefore situated over a single centrum, rather than being truly intervertebral. The transition from the condition in which spinal nerves pass through foramina in the pedicles to the condition in which they pass behind the pedicles appears to take place at vertebra 6. Variability of this feature is known in Recent taxa, with the transition occurring between the 15th and 21st vertebra in *Dermophis mexicanus*, and between the fifth and 11th in *Typhlonectes compressicauda* (Wake, 1980a). A small tubercle (anapophysis) along the posterior margin of the pedicle lies in close relation to the prezygapophysis of the following vertebra, and would seem to support the zygapophysis from below. The diapophysial facets are comparable in orientation and dimensions (0.8 and 0.4 mm along the long and short axes, respectively) to those on the axis, but they are not as protuberant. Rib heads in this region appear to have articulated with parapophysial hemifacets developed on the margins of adjoining centra anteroventral to the diapophysis. The postzygapophyses are interconnected by a bony lamina; zygapophysial facets appear to be less horizontally inclined than in more rostral vertebrae. The length of the vertebrae, measured between the tips of the pre- and postzygapophyses, is 2.7 mm. Nuchal keels appear to be low; the spinous process is represented primarily by an elevated area between the dorsal surfaces of the postzygapophyses.

Three ribs preserved on the right side of the sixth and seventh vertebrae appear to be associated with these vertebrae, but they are displaced from their articulations (Fig. 33B). The most anterior rib, which is fractured but complete, measures 3 mm from head to distal tip; the proximal shaft has a diameter of 0.38 mm and the centers of the capitular and tubercular facets are 0.8 mm apart. The successive ribs appear to be slightly more slender, but the proximal ends are unexposed, and the distal ends broken.

An isolated vertebra, lying less than 2 mm away from the atlas axis of the MCZ 9169 series, appears to have characteristics intermediate between the sixth and seventh vertebrae and another articulated series of four vertebrae. The isolated vertebra, tentatively identified as the eighth, has a centrum length of 1.8 mm, a pre- to postzygapophysial length of 2.8 mm, and a smaller diapophysial facet (0.5 and 0.2 mm along the long and short axes, respectively; the long axis is less vertically inclined). The pre- and postzygapophysial facets are inclined with respect to the horizontal by an estimated 20°.

A series of four articulated vertebrae, tentatively identified as the ninth through 12th, is characterized by longer centra (2.1 mm) and very faint nuchal keels, with a slight excrescence between the dorsal surfaces of the postzygapophyses representing the spinous process. Crescentic intercentra are present (anteroposterior thickness, 0.3 mm). The rib heads appear to have articulated with demifacets on adjacent superolateral margins of the ends of the centra. There are no diapophysial processes as such. Rather, tuberculi appear to have articulated in small, circular depressions (0.2 mm diameter) on the side of the pedicle, the centers of which are located 0.5 (on vertebra 11) to 0.6 mm (on vertebra 8) dorsocaudally from the capitular demifacets. Immediately posterior to each depression is a low tuberosity. Other features are comparable to those seen in PA5 and vertebrae 6 and 7, with the exception of the inclination of the zygapophysial facets. Crushing and distortion obviate precise measurement of facet angle, which is estimated to be at least 30° but not more than 45°. The ribs are shorter and more slender than those of more anterior vertebrae, and the capitulum and tuberculum are closer together. Ribs 10 and 11, the most completely preserved in the series, are 2.3 and 2.45 mm long and have proximal shaft diameters of about 0.3 mm; the

centers of the capitular and tubercular facets of rib 11 are separated by a distance estimated to be about 0.5 mm.

Two additional isolated vertebrae lie within several centimeters of the anterior dorsal series, but neither is sufficiently well preserved to be informative.

Two centimeters from the anterior dorsal vertebrae described above, a coiled but articulated series of 13 vertebrae is associated with shoulder girdle and forelimb elements (Fig. 35A). The principal features of more anterior dorsal vertebrae are maintained in this series, with only slight changes in proportions. The series can thus reasonably be interpreted as a continuation of the dorsal column, thus representing vertebrae 13 through 25. Measured lengths (in some cases estimated) of 10 centra range from 1.9 to 2.3 mm, with a mean of 2.12 mm, which is comparable to that observed in the anterior dorsal series; variations in length are random along the series and therefore appear to be due to preservational artifact. Total vertebral length, measured from the anterior end of the prezygapophyses to the posterior end of the postzygapophyses, appears to increase slightly. Measured or estimated lengths of seven specimens range from 3 to 3.4 mm, with a mean of 3.2 mm (the greatest overall length that can be measured in the anterior dorsal series is 2.9 mm at vertebra 8). An increase in size of the crescentic intercentra intercalated between the ventral margins of the notochordal centra appears to compensate for the increase in overall vertebral length when the length of the centra remains the same. Intercentra are 0.4–0.5 mm in anteroposterior thickness (versus 0.3 mm in the anterior dorsal region). As in more anterior dorsal vertebrae, the lateral and ventral aspects of the vertebral centra are concave; a faint median crest extends longitudinally along the ventral surface but does not reach the anterior or posterior ends. The orientation of zygapophysial facets in many cases is altered by postmortem plastic deformation; on well-preserved, symmetrical vertebrae, the facets lie at about 30° to horizontal. Spinous processes are absent; a narrow, low median crest extends longitudinally from a slight tuberosity between the bases of the prezygapophyses to a more prominent tuberosity between the postzygapophyses. The ribs associated with the fifth and twelfth vertebra of this series are slightly longer (length 2.65–2.7 mm) than those of more anterior dorsal ribs but are comparable in proximal shaft diameter (ca. 0.3 mm) and in the manner with which they articulate with the centra.

Middorsal Region. In addition to the postatlantal and anterior dorsal vertebrae described above, MCZ 9169 also includes two isolated series of more or less articulated vertebrae (on a separate block of matrix) that lack any direct evidence of axial position. The shorter series of four damaged vertebrae provides little useful information. The longer series represents 18 vertebrae, although the 12th was lost during the quarrying process. The vertebrae are morphologically similar, particularly in rib size and articulation, to those of the anterior dorsal series, with the exception that there is no indication of a median nuchal keel. The lengths of the centra, however, range from 1.9 to 2.0 mm (mean 1.95 mm), which is about 0.25 mm shorter than the lengths of the centra of the last several vertebrae in the anterior dorsal series. If MCZ 9169 comprises a single specimen, the middorsal region is morphologically similar to the anterior dorsal region save for shorter vertebrae and would be comparable to the gradual decrease in centrum and neural arch length in the middorsal and posterior dorsal regions of *Dermophis mexicanus* (Wake, 1980a). Alternatively, the series of 18 could represent the dorsal region of a slightly smaller individual.

Posterior Dorsal, Sacral, and Caudal Vertebrae. Right and left hindlimb elements are closely associated with a series of vertebrae in MNA V8062 (Fig. 36) and thus provide the evidence for identifying posterior dorsal and caudal vertebrae. Var-

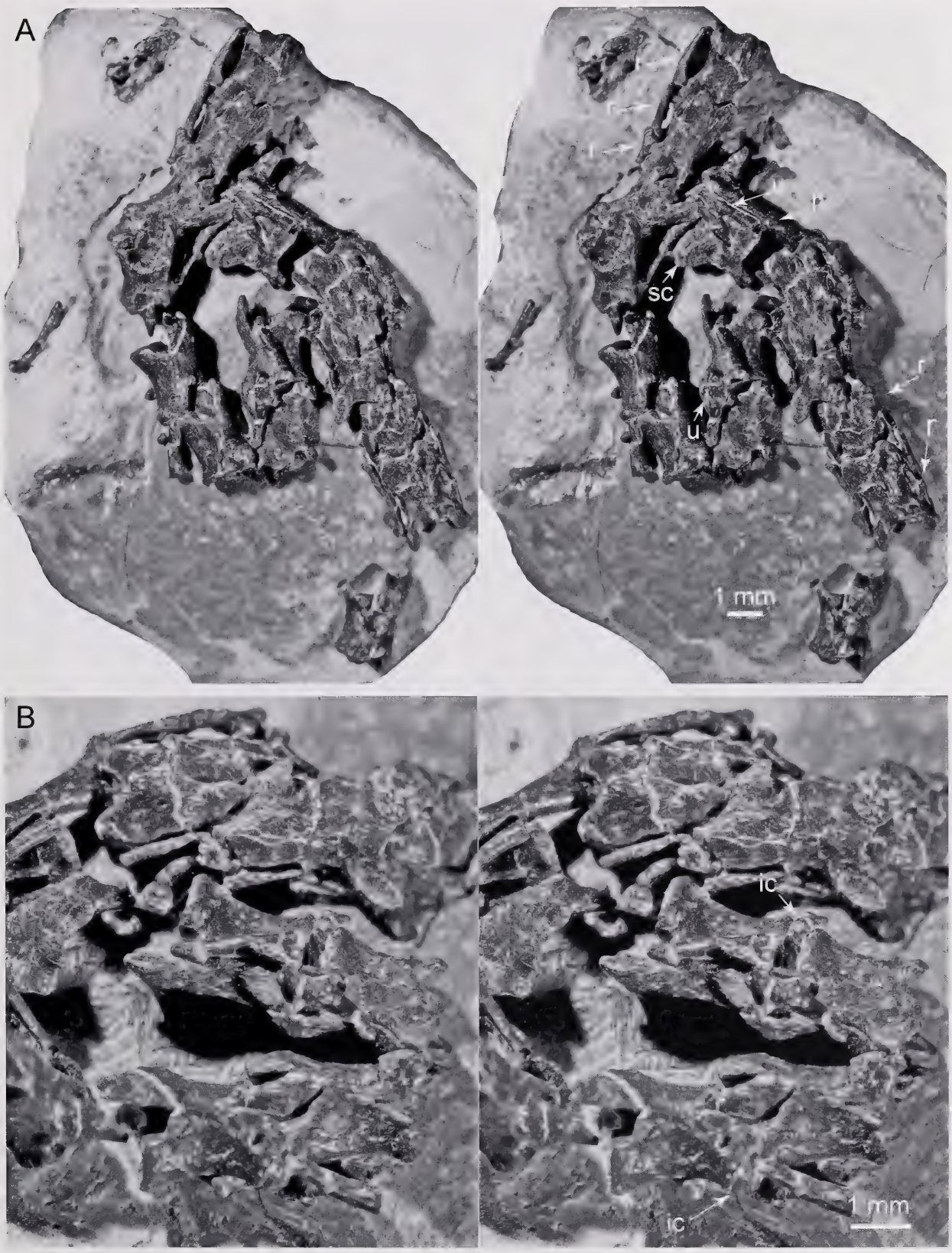

Figure 35. (A) Anterior dorsal vertebrae of *Eocaecilia micropodia* (MCZ 9169) associated with forelimb elements: scapulocoracoid, humerus, and ulna. (B) An enlargement to show the intercentra and details of the vertebrae (stereophotographs).

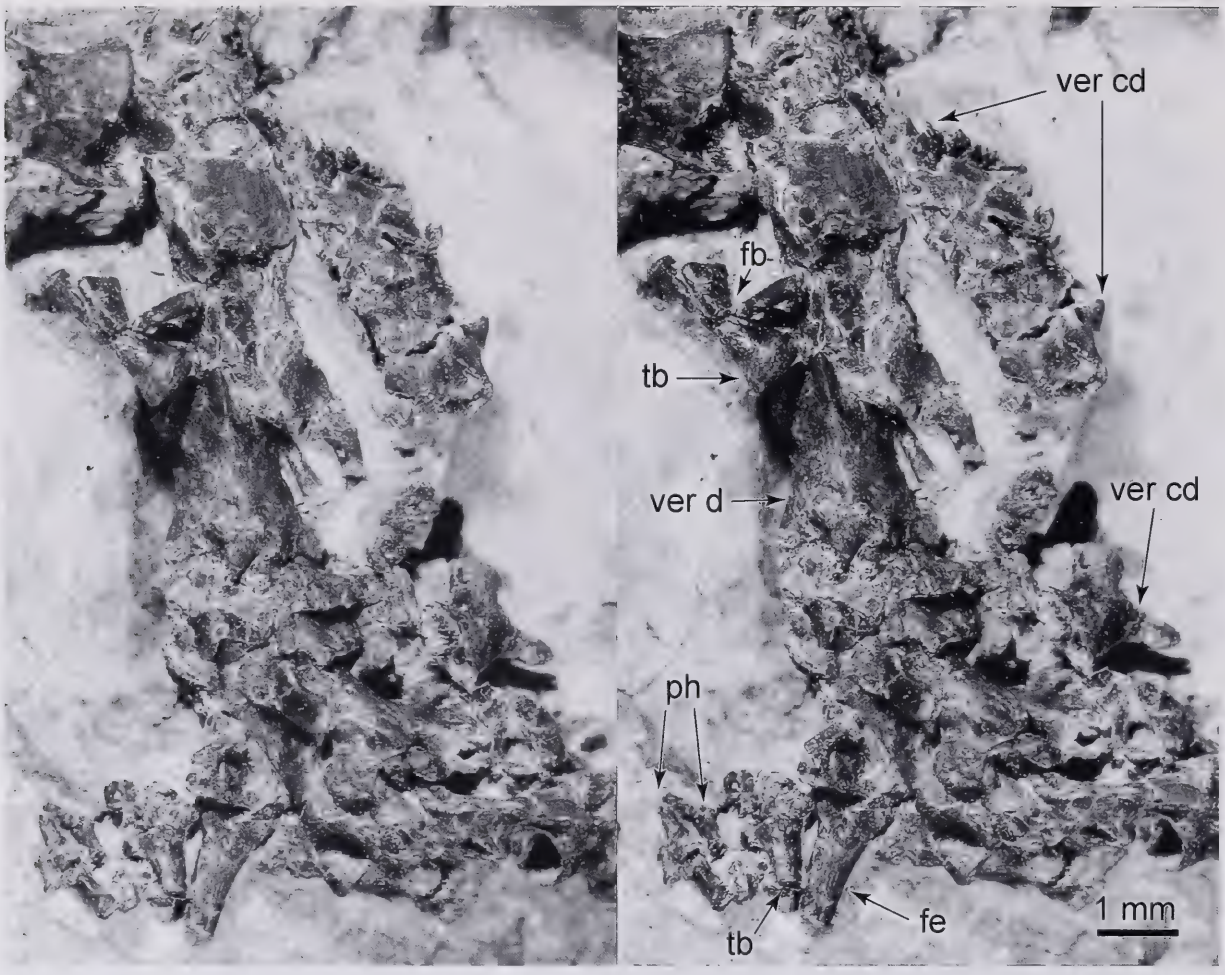

Figure 36. Posterior dorsal and caudal vertebrae, partial femur and ?fibula, and tibia and phalanges of *Eocaecilia micropodia* (MNA V8062; stereophotographs).

iable crushing and distortion of the entire series, however, substantially obscures many structural details. Only one (incomplete) rib is preserved with the posterior dorsals; this slender rib appears comparable to those of other dorsals, with the centers of the tuberculum and capitulum spaced 0.4 mm apart and a shaft diameter of 0.2 mm. The two vertebrae that are immediately adjacent to hindlimb bones are tentatively identified as sacrals. A characteristic sacral feature is the large size of the diapophyses, in contrast to those on posterior dorsal vertebrae that precede them (only four of which are sufficiently preserved to be useful for comparative analysis). In addition to the large size of the tubercular (diapophysial) facets, sacrals appear to differ from posterior dorsal vertebrae in being slightly shorter in overall length and narrower in interzygapophysial width. These features are preserved on the second sacral; the first sacral is largely crushed, and only posterior interzygapophysial width is preserved. Sacral centra are approximately 1.4 mm in length, whereas the centrum of the penultimate posterior dorsal is 1.7 mm; the third vertebra anterior to the penultimate has a centrum length of 1.8 mm. In typical dorsal vertebrae, tubercular facets are flush with the sides of the pedicles; on the putative sacrals, tubercular facets are elevated from the lateral surface of the pedicles and are thus borne on low diapophyses. On two posterior dorsals, the transverse distance between the lateral margins of the postzygapophyses is 1.4 mm, compared with about 1 mm on the two sacrals.

Proximal caudals in MNA V8062 appear

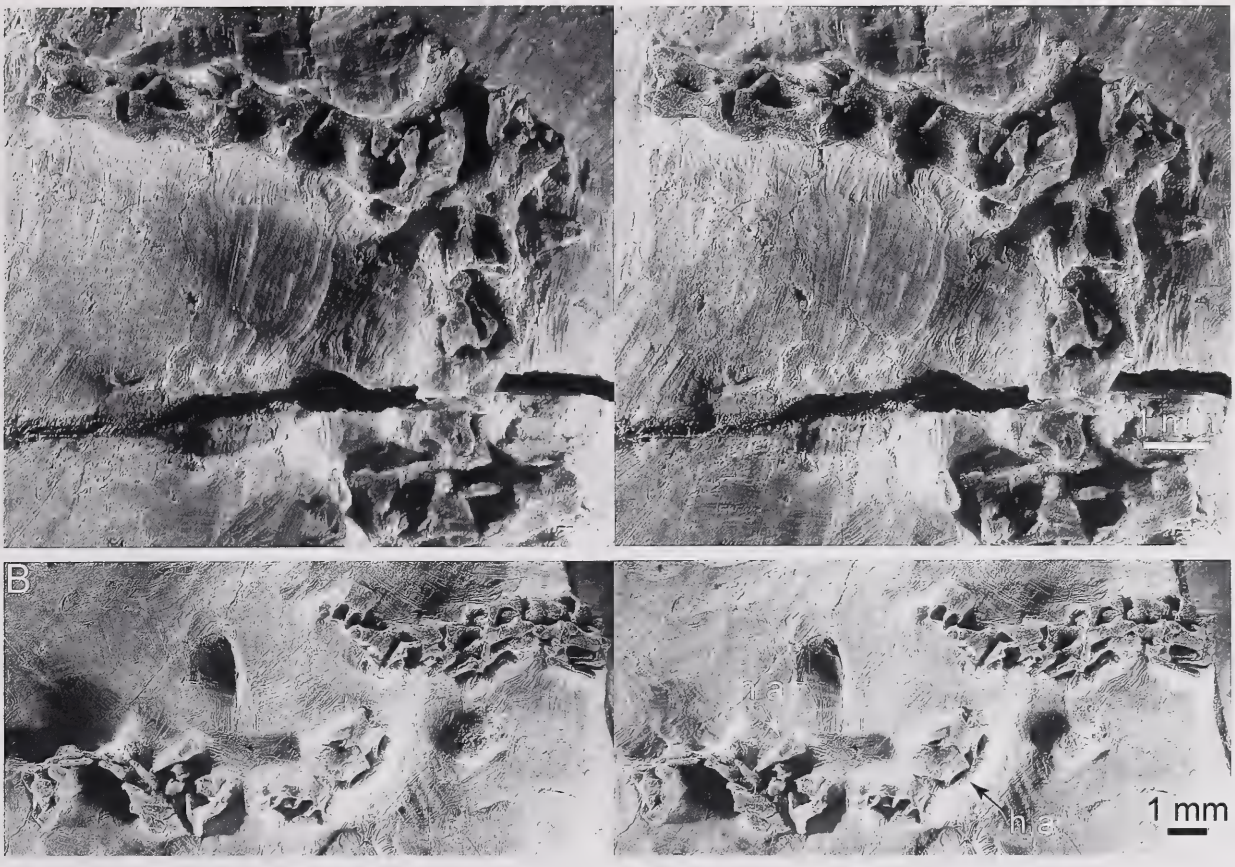

Figure 37. (A) Dorsal vertebrae, (B) caudal vertebrae of *Eocaecilia micropodia* (MNA V8055; stereophotographs).

to have centrum lengths comparable to those of the sacrals (1.4 mm) but have zygapophyses that project dorsally, in contrast to more horizontally inclined processes of dorsal and sacral vertebrae. Distal caudal vertebrae are represented by a single, disarticulated vertebra and an attenuating series of approximately eight vertebrae. The single vertebra has a centrum length of 1.1 mm and bears a prominent, posteriorly recurved, tapering spinous process. The terminal series of vertebrae is very damaged but exhibits a diminishing length gradient of the centra from about 0.7 to 0.4 mm.

MNA V8055 preserves some 30 vertebrae, a number of which occur in articulated series. One series of 12 vertebrae appears to be continuous, although the continuity is disrupted between the sixth and seventh by a disarticulation to a right-angle bend (Fig. 37A). A few slender rib fragments are associated, and the lengths of the centra diminish from about 2 mm anteriorly to 1.55 mm posteriorly; this series appears to represent the dorsal or very possibly posterior dorsal region. Five isolated vertebrae, including two that are articulated, also appear to be dorsals; other isolated vertebrae are too imperfectly preserved to be useful. Caudal vertebrae (Fig. 37B) are represented in a more or less articulated series of 10, with the lengths of the centra diminishing from 1.3 mm on the most anterior to approximately 1 mm on the penultimate. The zygapophyses on the anterior three are small and set close to the midline; distal to the fifth vertebra, zygapophysial articulations are reduced to a simple overlap of a lamina with that of the vertebra behind. Several well-developed haemal arches are associated with this series. The haemals are conventional in structure, tapering from a broad, perforate base (0.6 mm in width) to the distal apex (1.7–1.8 mm in overall length). Among living caecilians, haemal arches are known only in the rhinatrematid *Epicrionops* (Wake, 1987b, 2003, fig. 22A; Carroll

et al. 1999, fig. 6A). The last five vertebrae in this series bear a posteriorly recurved, tapering spinous process comparable to those present in the terminal series of caudals in *Epicrionops bicolor* (Wake, 2003, fig. 22A). The caudal series of MNA V8055 is incomplete, however. The terminal vertebrae of *Eocaecilia micropodia,* known only in MNA V8062 (Fig. 36), exhibit recurved processes that decrease in size and are lost altogether as the vertebrae are reduced to tiny cylindrical structures.

Comparative Anatomy of the Vertebral Column. The vertebral column of *Eocaecilia micropodia* differs from those of Recent gymnophionans in the presence of intercentra, an interglenoid tubercle on the atlas, and most notably in the absence of the various elaborate processes that occur in modern forms. Gymnophionans typically possess a longitudinal keel or process along the ventral aspect of the centra, anteriorly projecting parapophysial processes, and postzygapophyses that are interconnected by an extension of the laminae which overlay the following vertebra; neural spines are absent except on anterior vertebrae, where there is a longitudinal nuchal keel. Of these features, *E. micropodia* possesses the postzygapophysial interconnection and overlap, but only the faintest representations of ventral and nuchal keels. With the exception of the postatlantal region, in which there are distinct diapophyses, costal tubercles articulate with facets that are only slightly raised from the surface of the pedicles. The first rib has a capitular articulation on the atlantoaxial intercentrum, but other capituli appear to articulate with pairs of hemifacets developed on adjacent centra, with no elaboration of parapophyses or other processes. Intravertebral neural foramina are present on the atlas and at least the following four vertebrae. Last, the prominent, posterodorsally reflected spinous processes on distal caudal vertebrae of *Eocaecilia* are a feature shared with the rhinatrematid *Epicrionops* (Wake, 2003, fig. 22A).

The vertebral structure of *Eocaecilia micropodia* appears to be generally more primitive than that represented by eight isolated vertebrae of an early Cretaceous caecilian, *Rubricacaecilia monbaroni,* described by Evans and Sigogneau-Russell (2001). *Eocaecilia micropodia* does share certain features with *R. monbaroni*: amphicoelous centra, an increase in centrum length from the postatlantal into the dorsal series, a low nuchal keel on anterior vertebrae, and circular, low diapophyses. However, *E. micropodia* does not exhibit any parapophysial processes or basapophyses, which in *R. monbaroni* would seem to represent an incipient stage in the distinctively gymnophionan elaboration of these structures. Furthermore, the midventral region of the centra in *R. monbaroni* is narrowed to a keellike ridge, of which there is only a faint indication in *E. micropodia.*

Had *Eocaecilia micropodia* attained the distinctively high vertebral counts of modern caecilians? Published estimates of the range of vertebral counts across living taxa vary slightly. Without citing specific taxa, Nussbaum and Naylor (1982) state that vertebral numbers in gymnophionans range from 70 to 283, whereas Wake (1980a) and Duellman and Trueb (1986) cite postatlantal vertebral counts of 95–285. Most recently, Wake (2003) cited 86–285. Taylor's (1968) monograph, however, reports specific counts for individual species; the lowest occur among various specimens of *Epicrionops* (e.g., *E. bicolor subcaudalis,* 75–78; *E. lattivittatus,* 78) and the highest in *Oscaecilia bassleri* (273). Given that vertebral numbers vary intraspecifically (Taylor, 1968), a more precise determination of the range would seem to offer little utility, especially in the context of a comparison with *E. micropodia,* for which a vertebral count can only be estimated. The most complete specimen (MCZ 9169) comprises five series of more or less articulated vertebrae, representing the postatlantal, anterior dorsal, and most probably, dorsal regions. The total number

of vertebrae is 49 if several associated but isolated vertebrae are included. MNA V8062 provides an imperfect representation of the sacral and caudal regions. On the assumption that the identification of two sacral vertebrae is correct (these vertebrae are most closely associated with the hindlimb elements), there are at least 13 caudals. A minimum estimate of the total vertebral count in *E. micropodia* is therefore 64. Although the anterior and posterior ends of the column can be enumerated, there is no specimen in which a vertebral series links the fore- and hindlimbs, and thus the count in the dorsal region is uncertain. Our conclusion is that vertebral numbers in *E. micropodia* certainly approached, and very possibly nested within, the lower end of the range of variation known among modern caecilians.

Appendicular Skeleton

Anatomical Location of the Forelimb. As noted above, shoulder girdle and forelimb elements in MCZ 9169 are associated with an articulated series of 13 dorsal vertebrae (Fig. 35A) that likely represent the 13th through 25th vertebrae. The limb bones, although clearly associated, are rather completely disordered (Fig. 38); thus, they provide no definitive evidence that the forelimb was anatomically situated at this point in the dorsal series. The occurrence of an isolated radius lying on PA4 of MCZ 9169 confirms that limb bones were displaced in this specimen. Although the actual position of the girdle and forelimb remains uncertain, the scapulocoracoid is here reconstructed in relation to more anterior dorsal vertebrae (Fig. 31). The occurrence of various shoulder and forelimb elements with numerous cranial specimens (MCZ 9163, 9167, 9171, 9237, 9242; MNA V9056, V8065) is suggestive evidence that the forelimb was positioned closer to the head than the association of MCZ 9169 might imply.

Scapulocoracoid (MCZ 9237, 9238, 9169, 9171; MNA V8056, V8059, V8064, V8065). The two most completely known scapulocoracoids of *Eocaecilia micropodia* (MNA V8056, MCZ 9237, Fig. 39B, C) are 3 mm in height, measured from the dorsal margin of the scapula to the posteroventral margin of the coracoid. The scapular blade is narrowly constricted at its midpoint, which is oval in cross section (Fig. 39). Dorsally, the blade is expanded and ends as a convex margin of trabecular bone indicative of its continuity with a suprascapular cartilage (Fig. 39A). The base of the scapula bears an oval glenoidal facet that faces posteroventrally and slightly laterally (Fig. 38) and an anteriorly directed process that is incised ventrally. The margin of the anterior process, like the dorsal margin of the scapular blade, appears to have been continued in cartilage; thus, the incisure was probably enclosed to form a coracoid foramen. The suture between the scapula and coracoid is preserved as a faint lineation that passes from the incisure across the glenoid. The coracoid bears an approximately circular, dorsolaterally facing glenoidal facet (Fig. 38); the remainder of the coracoid is an approximately rectangular plate of very thin bone and is preserved, in crushed condition, in only two specimens (Fig. 40). The scapular and coracoidal ends of the glenoid facet, which have very different orientations, are connected by a narrow, intermediate part of the glenoid that turns a spiral from one end to the other. The spiral configuration of the glenoid in *E. micropodia* is thus similar to the pattern common among Paleozoic tetrapods. Ventral to the anterior half of the glenoid is a circular fossa of unknown function. A fossa in a similar position occurs in a few microsaurs (e.g., *Asaphestra,* Carroll and Gaskill, 1978: 173–174, fig. 8C; *Batropetes,* Carroll, 1991: 238, fig. 6A), but there is no compelling evidence that these features are strictly comparable.

Humerus (MCZ 9163, 9166, 9167, 9171, 9237, 9238; MNA V8056, V8068). Complete humeri vary in length from 4.25 mm (MCZ 9169) to 4.4 mm (MCZ 9163, Fig. 41). The bulbous head extends from the

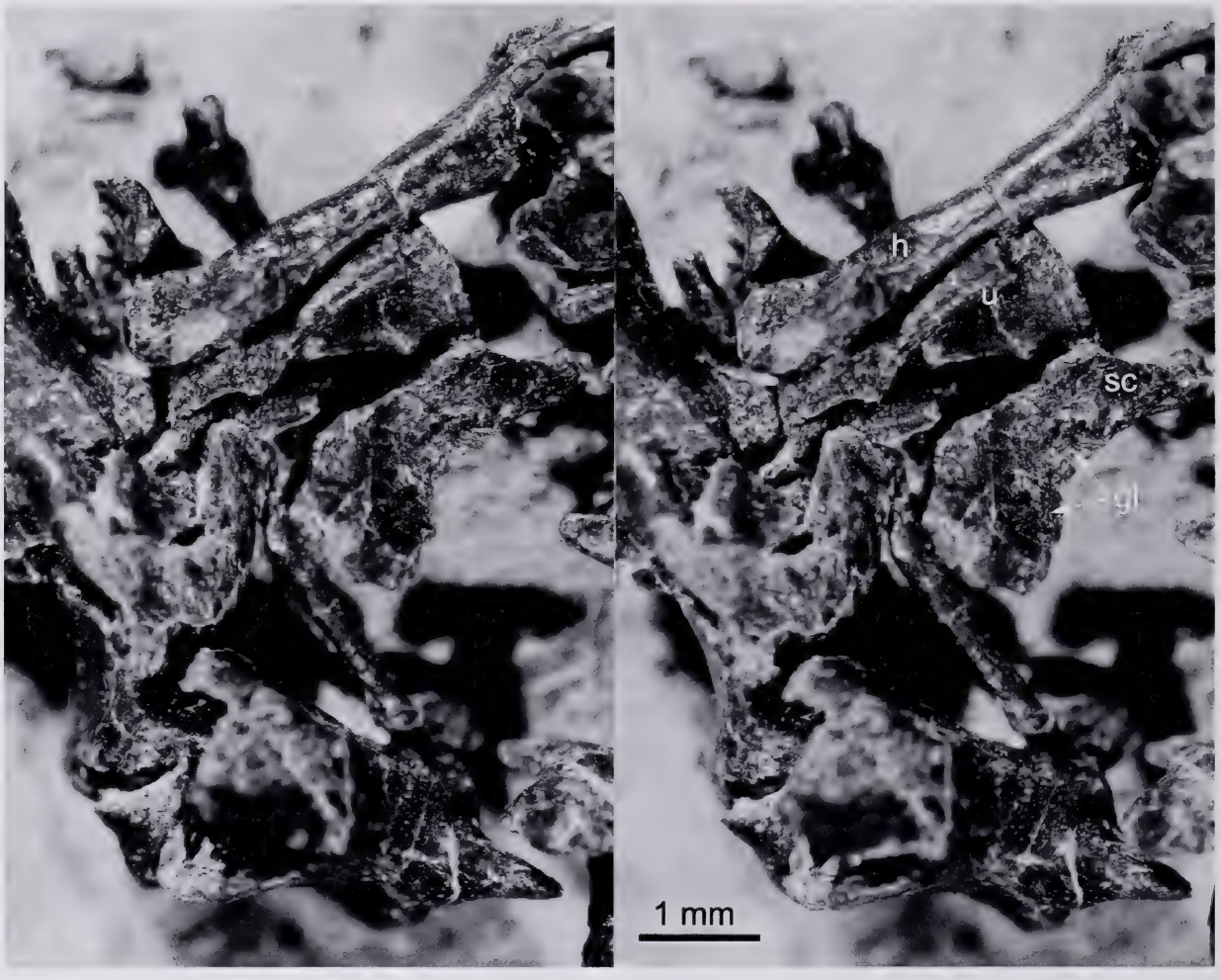

Figure 38. Forelimb elements of *Eocaecilia micropodia* (MCZ 9169), an enlargement of Figure 35A to show details of the scapulocoracoid, glenoid, humerus, and partial ulna. The upper and lower arrows indicating the glenoid (gl) point, respectively, to the scapular and coracoidal components of the glenoid facet (stereophotographs).

dorsolateral to the ventromedial surfaces of the proximal end in a spiral pattern common among Paleozoic amphibians (Fig. 42A–D; also present in MCZ 9166). The deltopectoral crest in an apparently undistorted humerus is reflected ventrally (Fig. 38) and is continuous with a low ridge that extends proximally. A small tuberosity on the dorsomedial side of the proximal diaphysis (Fig. 42C, D) is comparable in position to that in some microsaurs (e.g., *Cardiocephalus, Pantylus, Ricnodon,* Carroll and Gaskill, 1978, figs. 122A, B, 123D). In Recent *Salamandra,* a similar tuberosity serves as the site of insertion of subscapular musculature (Francis, 1934). Complete humeri (Figs. 38, 41) exhibit a simple shaft that is approximately circular in cross section. The distal end of the humerus bears a bulbous, hemispheroidal capitulum for the proximal radius and a broad but distinct trochlea for the proximal ulna (Fig. 42E; see also MCZ 9169, 9172). The ectepicondyle is represented only as a low ridge. The entepicondyle, in contrast, is a relatively robust protuberance that is prolonged distally; there is no entepicondylar foramen. Along the margin of the proximal border of the capitulum, the diaphysis is incised with a deep, hemicircular sulcus that presumably accommodated the radius in its most flexed position. MNA V8056 includes an associated distal humerus and a proximal radius and ulna that lie in nearly articulated position.

Radius (MCZ 9242, 9169; MNA V8056). A radius presumptively associated with an

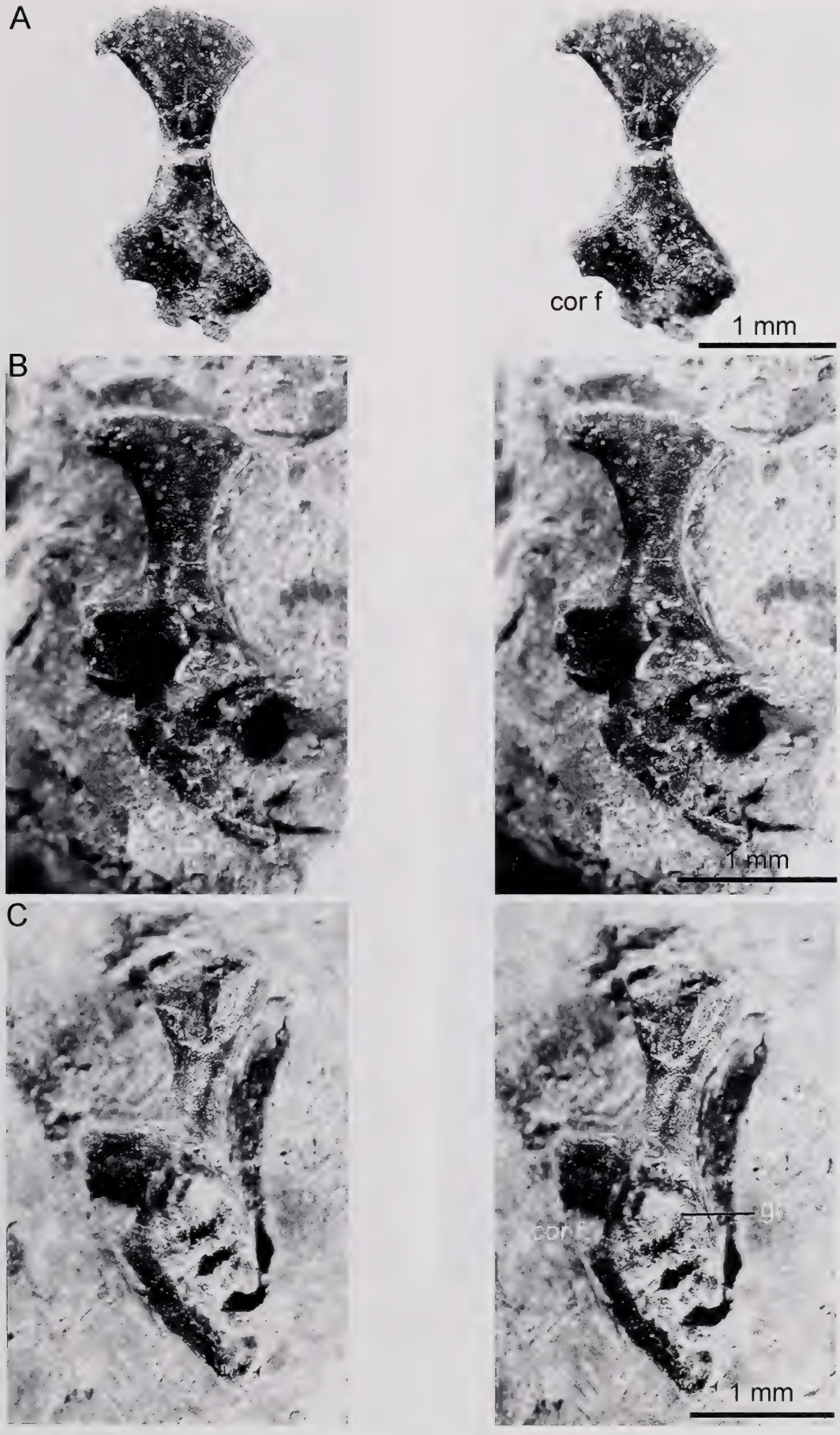

Figure 39. Left scapulocoracoids of *Eocaecilia micropodia* in lateral view: (A) MCZ 9238, (B) MNA V8056, (C) MCZ 9237. The coracoids are incomplete in all three specimens (stereophotographs).

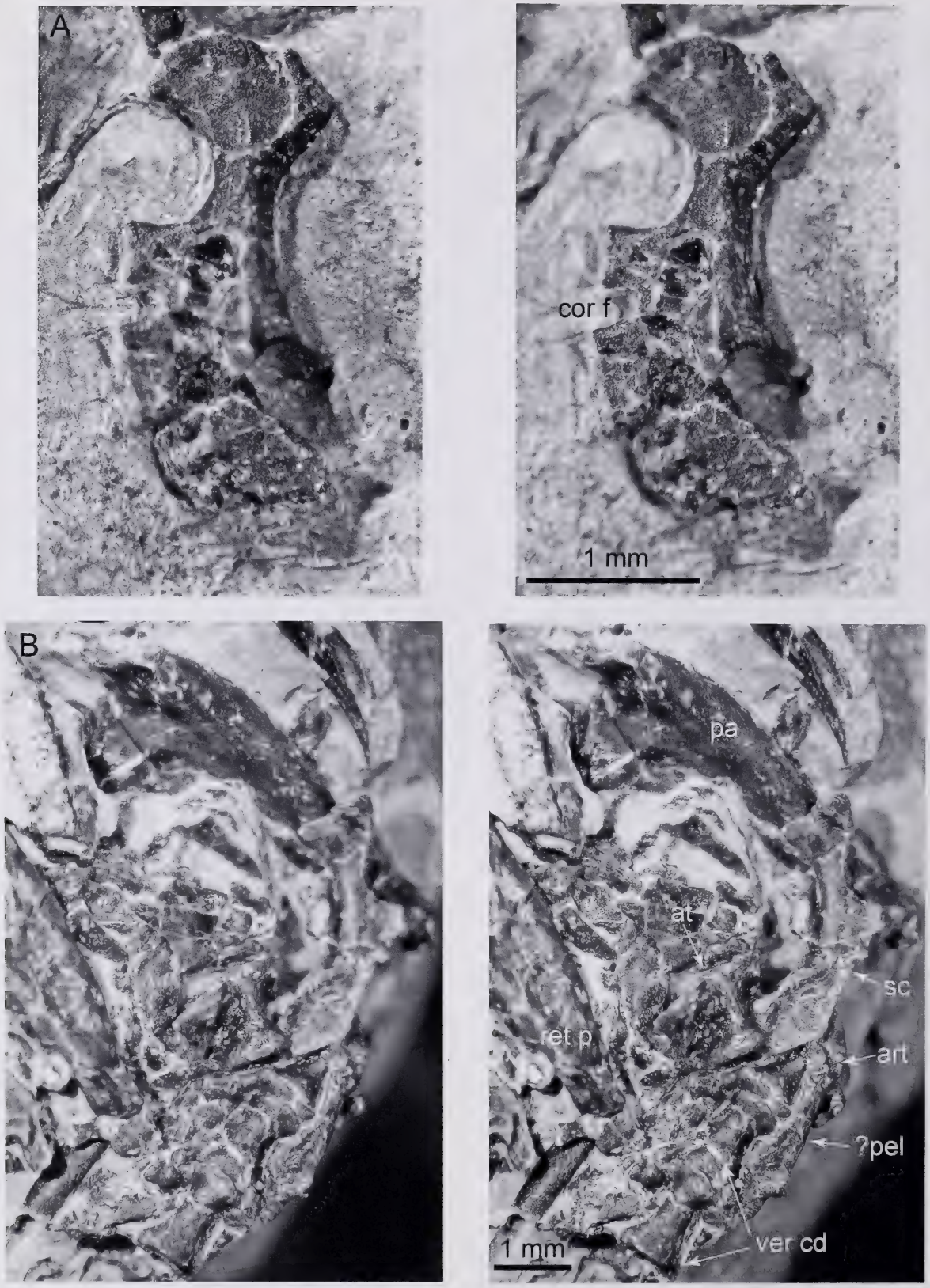

Figure 40. Scapulocoracoids of *Eocaecilia micropodia* with complete, although crushed, coracoids. (A) A left scapulocoracoid in lateral view (MNA V8064); the glenoid region has been damaged postmortem. (B) A left scapulocoracoid (in a medial view) and associated skeletal elements in MCZ 9171 (stereophotographs).

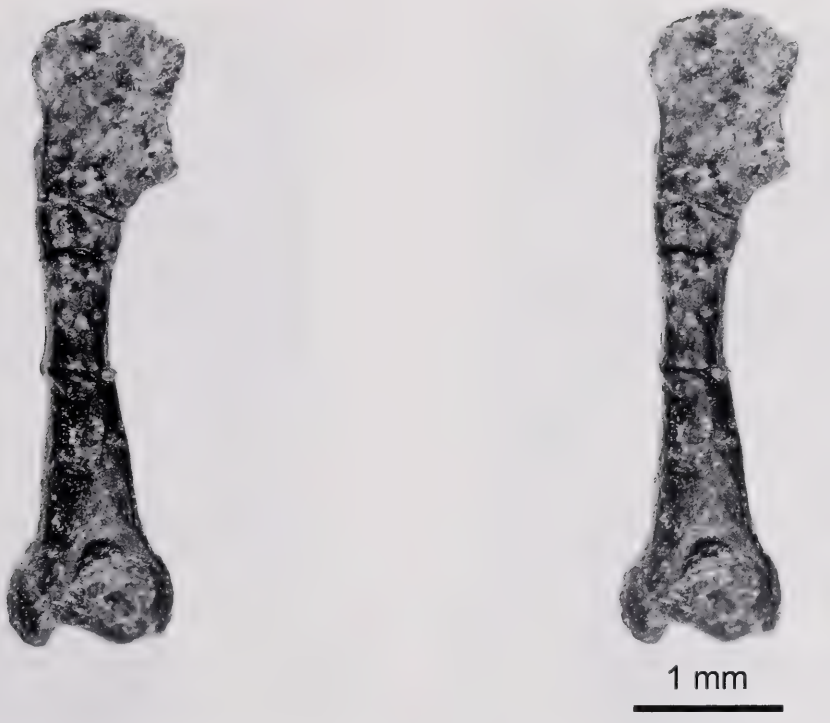

Figure 41. A complete left humerus of *Eocaecilia micropodia* (MCZ 9163) in ventral view. The specimen has been slightly crushed, with the deltopectoral crest deflected from the normal ventral orientation (stereophotographs).

ulna (MCZ 9242, Fig. 43A) is 2.16 mm in overall length. The surface of the proximal facet is set at an angle of about 20° to a plane normal to the shaft. The length of the radius measured from the most distal margin of the articular facet is 1.9 mm. Diaphyseal width narrows at midshaft to 0.39 mm, with the proximal end of the radius being more expanded than the distal end. The smaller distal articular facet is oval in outline and is set almost perpendicular to the shaft.

Ulna (MCZ 9163, 9167, 9169, 9238, 9242; MNA V8054, V8065). Complete ulnae vary in length from 2.1 mm (MCZ 9163) to 2.2 mm (MNA V8065, MCZ 9242). The proximal articular facet is asymmetrically biplanar, with the larger of the two demifacets being on the radial side (Fig. 43B). The olecranon process is short but distinct. The ulna is relatively broad, both mediolaterally and anteroposteriorly at its proximal end, and tapers to its narrowest point at midshaft. The distal end is only slightly expanded and bears a circular articular facet set perpendicularly to the shaft.

Manus. Although various mesopodial, metapodial, and phalangeal elements are associated with several disarticulated specimens of *Eocaecilia micropodia,* none can be confidently attributed to the manus.

Pelvis. No pelvic elements can be positively identified. MCZ 9171 is a disaggregated assemblage that includes jaws, an atlas, a scapulocoracoid, and several caudal vertebrae (Fig. 40B). Adjacent to the caudal vertebrae is a bladelike bone that is not comparable to any other known skeletal element in *Eocaecilia.* The bone (?pel, Fig. 40B) widens at one end, is narrower in the middle, and bears a concave articular facet, as well as a margin that is broken, at the other end, inviting speculation that the facet could be acetabular. The bladelike, rather than platelike, nature of the element is suggestive of an ilium, but in view of the lack of any comparative data on the pelvis of primitive caecilians, such an inference is entirely conjectural. Some crushed bone associated with the hindlimbs of MNA V8062 (Fig. 36) might represent a pelvis, but the state of preservation is uninformative.

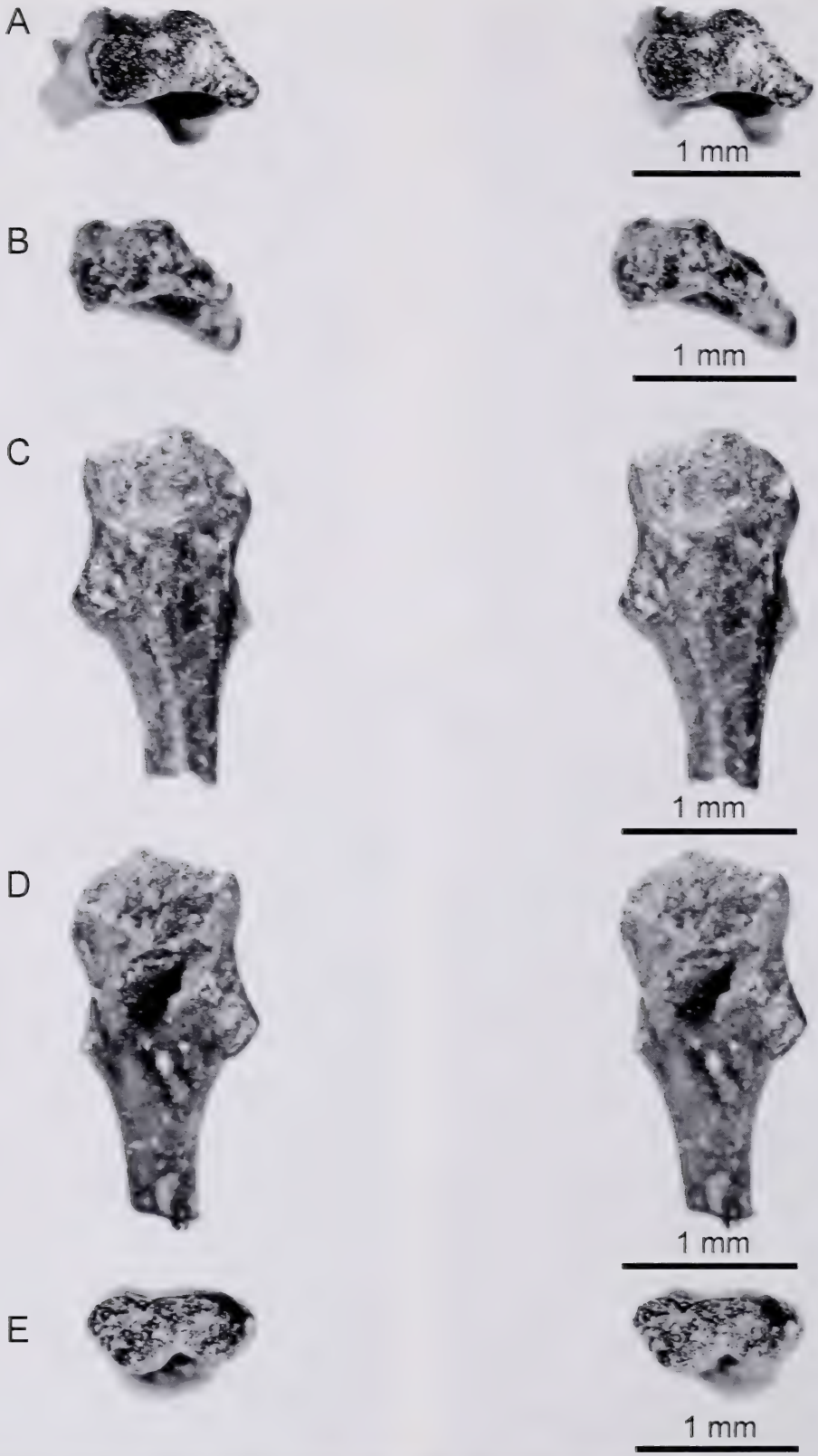

Figure 42. The humeral articular surfaces of *Eocaecilia micropodia*. (A) A left humeral head in proximal view (MCZ 9171). (B) A left humeral head in proximal view and in slightly lateral aspect (MCZ 9237). (C) Dorsal and (D) ventral views of a left proximal humerus (MCZ 9171). (E) A left distal humerus (MCZ 9237) in end view (stereophotographs).

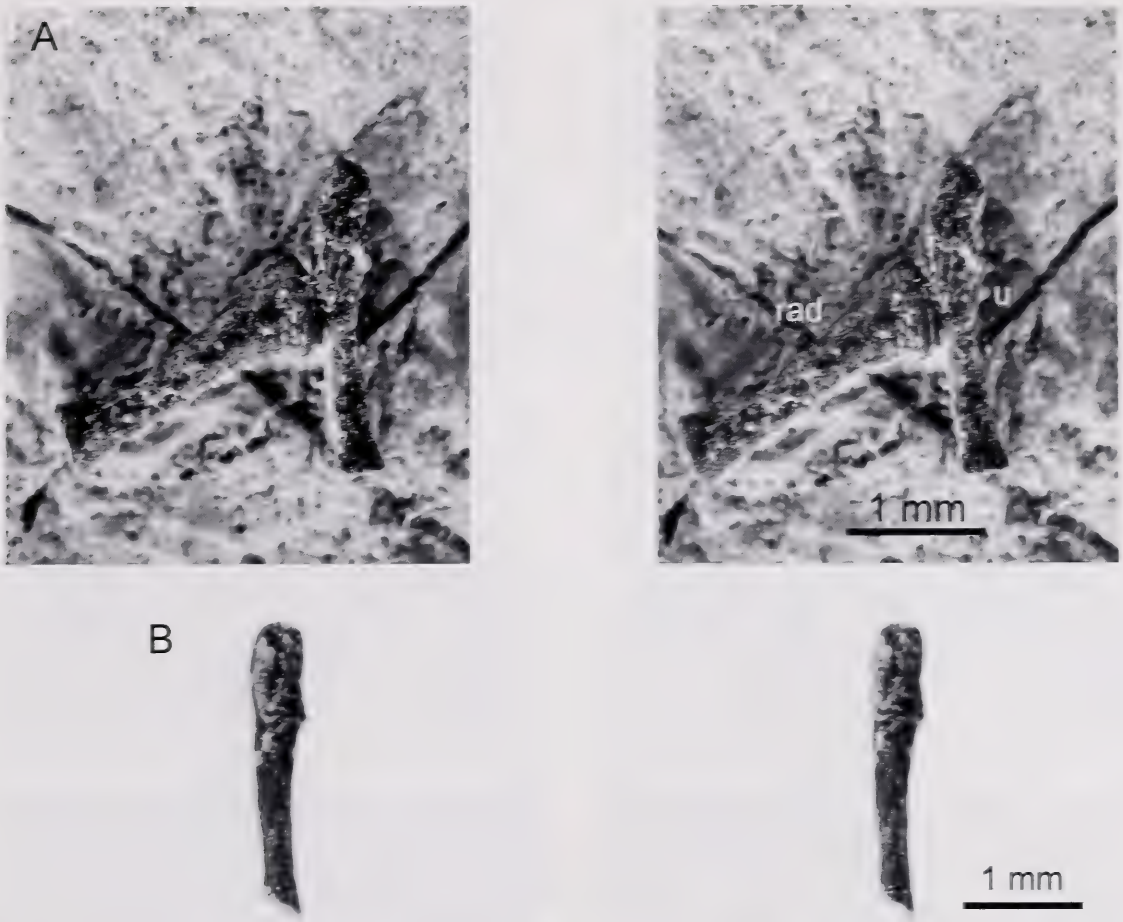

Figure 43. The antebrachial bones of *Eocaecilia micropodia*. (A) A presumptively associated left radius and ulna (MCZ 9242). (B) Proximal left ulna (MCZ 9238) in anterior view (stereophotographs).

Femur (MNA V8055, V8062). A complete left femur (Fig. 44) is 4.4 mm in length and has a midshaft width of 0.4 mm. The bulbous, approximately oval femoral head is oriented primarily dorsoventrally but is slightly skewed, such that the dorsal half is more anteriorly situated than the ventral half. On the medial and lateral sides of the head are shallow depressions, comparable to the foveae of some salamanders that represent the attachments of acetabular ligaments from the pubis and ilium (Francis, 1934, pl. V, fig. 32). A prominent, triangular trochanter is situated on the medioventral side of the proximal shaft. The expanded distal end, which is somewhat damaged (estimated width 1 mm), bears two condyles separated by an intercondylar groove. The lateral condyle is wider and more protuberant and possesses a larger radius of curvature than the medial condyle (Fig. 44C). The lateral epicondylar region is distinctly convex and facetlike, features that probably represent the articular surface for the fibula (Fig. 44B). In overall proportions and, specifically, in the configuration of the femoral head, the foveae, and the trochanter, the femur of *Eocaecilia micropodia* is similar to that in certain modern salamanders (for a comparative illustration, see Jenkins and Walsh, 1993, fig. 1h, i). The femoral head distinctly differs from those of microsaurs and other Paleozoic amphibians, which are anteroposteriorly elongate.

Tibia (MCZ 9237; MNA V8055, V8062). A complete tibia associated with MNA V8062 (Fig. 36) is 2.1 mm in length with a midshaft diameter of 0.4 mm; the tibia associated with MNA V8055 (Fig. 45B) is 1.85 mm in length. The transversely expanded proximal end bears a slightly con-

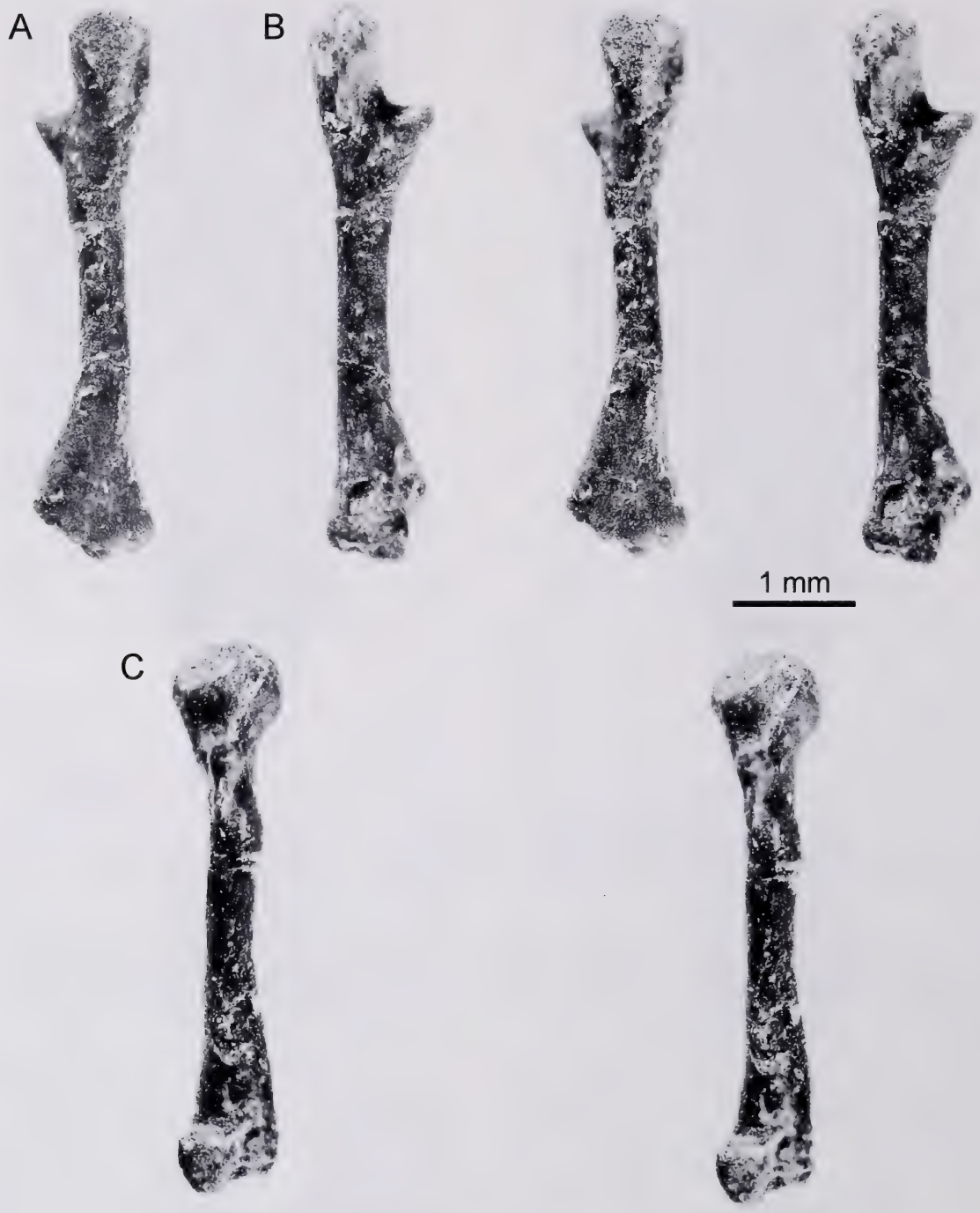

Figure 44. A complete left femur of *Eocaecilia micropodia* (MNA V8062) in (A) dorsal, (B) ventrolateral, and (C) ventral views (stereophotographs).

vex articular facet that accommodates both femoral condyles; the anterior edge of the facet slopes anteriorly and is bordered by a raised lip. A slightly raised area on the proximal, anterior surface of the shaft appears to represent a cnemial tuberosity (Fig. 45A). The distal articular facet is circular in outline and convex.

Fibula (MCZ 9237; MNA V8055, V8062). Fibular lengths range from 1.9 mm (MCZ 9237) to 2.1 mm (MNA V8055); midshaft diameter of the former is 0.3 mm. In both specimens, the fibula appears to have been preserved in an articular relationship with the tibia (Fig. 45). In both cases, the proximal articular facet, the plane of which is set at an angle of about 45° to the shaft, lies proximal to the

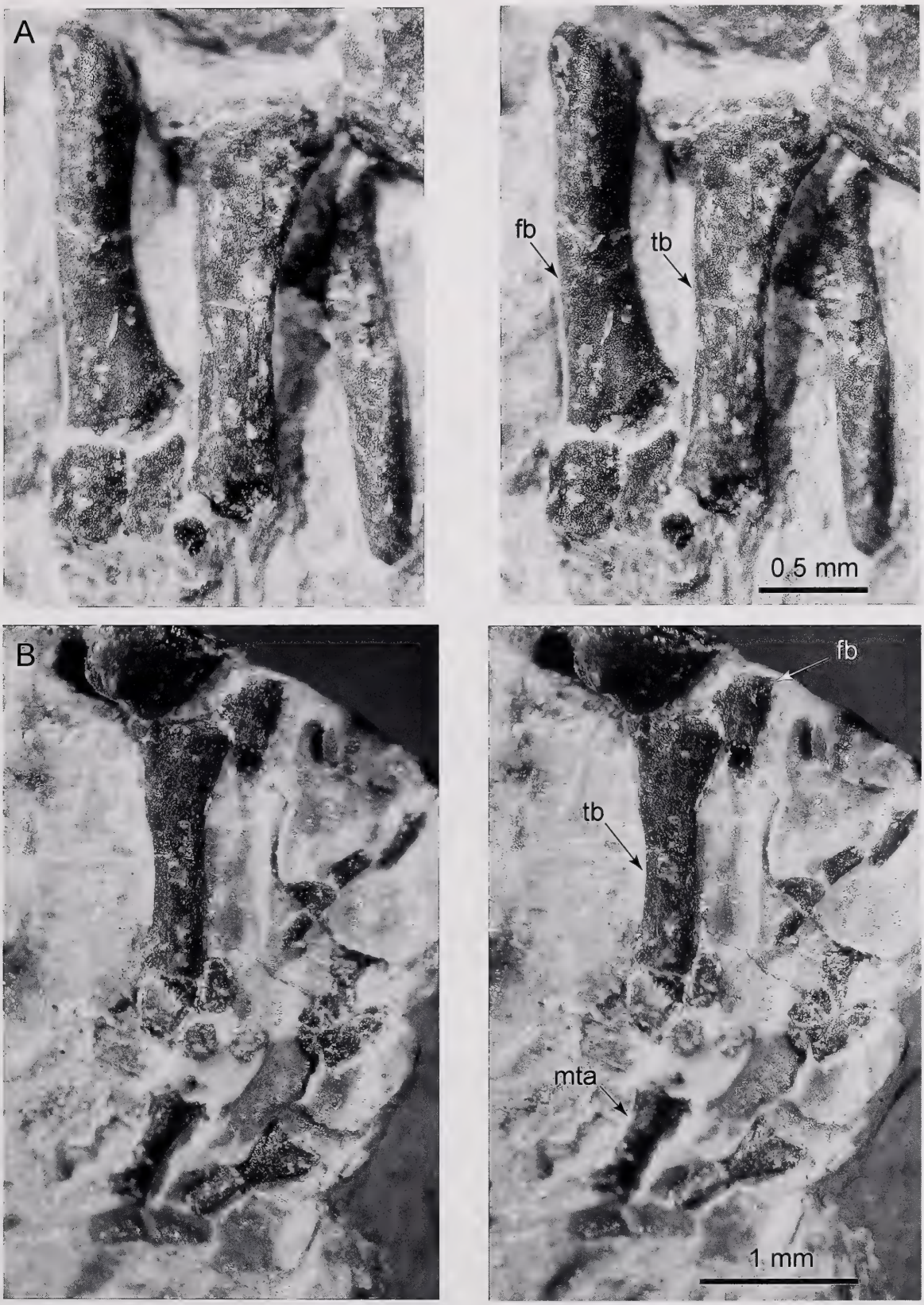

Figure 45. A tibia, fibula, and incomplete tarsus of *Eocaecilia micropodia.* (A) Anterior view of a right tibia and fibula (MCZ 9237) preserved in normal anatomical position, associated with the distal end of the femur (above) and three tarsals (below). (B) A presumptively right tibia in posterior view (MNA V8055). The specimen includes a distal fragment of the associated femur, a proximal fibula preserved in normal anatomical position (the remainder of the fibula, lost during excavation, is represented by a matrix mold), four tarsals, and several metatarsals (stereophotographs).

end of the tibia, evidence that the fibula articulated with the lateral epicondylar region of the femur. The fibular diaphysis is bowed laterally. Distally, the expanded end of the fibula terminates well short of the distal end of the tibia and bears two facets for contact with a fibulare and intermedium.

Pes (MCZ 9237; MNA V8055, V8056, V8062, V8073). MCZ 9237 and MNA V8055, taken together, demonstrate that the proximal tarsal row comprised a tibiale, intermedium, and fibulare (Fig. 45A, B). A partial pes associated with MNA V8062 (Fig. 36) shows that at least some digits possessed three phalangeal bones; the most proximal phalanx of the presumptively middle digit has a length of 0.89 mm and an estimated midshaft diameter of 0.25 mm. It is likely that *Eocaecilia micropodia* possessed only three digits because of the occurrence in several specimens (MNA V8056, V8062, V8073) of triads of phalanges.

DISCUSSION

Jaw Mechanics. Eocaecilia micropodia already possessed many of the major skeletal features of the jaw apparatus that are retained in Recent gymnophionans (e.g., prominent retroarticular process, pseudoangular and pseudodentary, internal process of the pseudoangular, mandibular fossa in close proximity to the jaw joint). These structural similarities invite the inference that the basic pattern of jaw muscles known from living gymnophionans had been developed as well.

Bemis et al. (1983) described various aspects of the feeding apparatus in *Dermophis mexicanus* (skull, lower jaw and articulation, teeth, hyobranchial apparatus, oral cavity and tongue, and jaw muscles) and confirmed the mechanics of the jaw through electromyography. Jaw closure is achieved not only by conventional action of the adductors, but through a gular muscle, the interhyoideus posterior, that acts to lower the retroarticular process (Fig. 46A; cf. Nussbaum, 1977). Jaw opening is accomplished by the depressor mandibulae, which passes from the back of the skull to an insertion on the retroarticular process. Nussbaum (1983) described the relative size of individual jaw muscles in representatives of four families (Rhinatrematidae, Ichthyophiidae, Caeciliidae, and Scolecomorphidae) and presented an analysis of the uniquely caecilian feeding apparatus.

To provide a more specific basis for interpreting the jaw mechanics of *Eocaecilia,* we review here additional details of the cranial muscles in an extant caecilian, *Ichthyophis glutinosus,* which was selected for this purpose as a relatively basal taxon. *Ichthyophis glutinosus* resembles other gymnophionans, with the exception of rhinatrematids, in the relatively large size of the interhyoideus posterior and the relative reduction of the adductors (Nussbaum, 1983, fig. 2). The retention of pre- and postfrontals in ichthyophiids is a primitive feature; they are lost or fused in most other gymnophionans. The derivation of the family Ichthyophiidae as being close to the base of the crown group gymnophionans is supported by morphological (Nussbaum, 1979) as well as molecular data (Hedges et al., 1993; San Mauro et al., 2004).

Four divisions of the adductor mandibulae can be recognized: adductor mandibulae externus, adductor mandibulae internus, adductor mandibulae posterior (which includes a levator quadrati), and pterygoideus (Fig. 46B–E). The first three are oriented essentially vertically and can be recognized primarily on the basis of their separation by branches of the trigeminal nerve.

The adductor mandibulae externus (AME) is the largest and most superficial in position, lying lateral to the maxillary branch of the trigeminal nerve (Fig. 46B). Originating on the ventral surface of the skull roof, the muscle converges ventrally to insert on a small area of the pseudoangular that includes the mandibular fossa.

The adductor mandibulae posterior

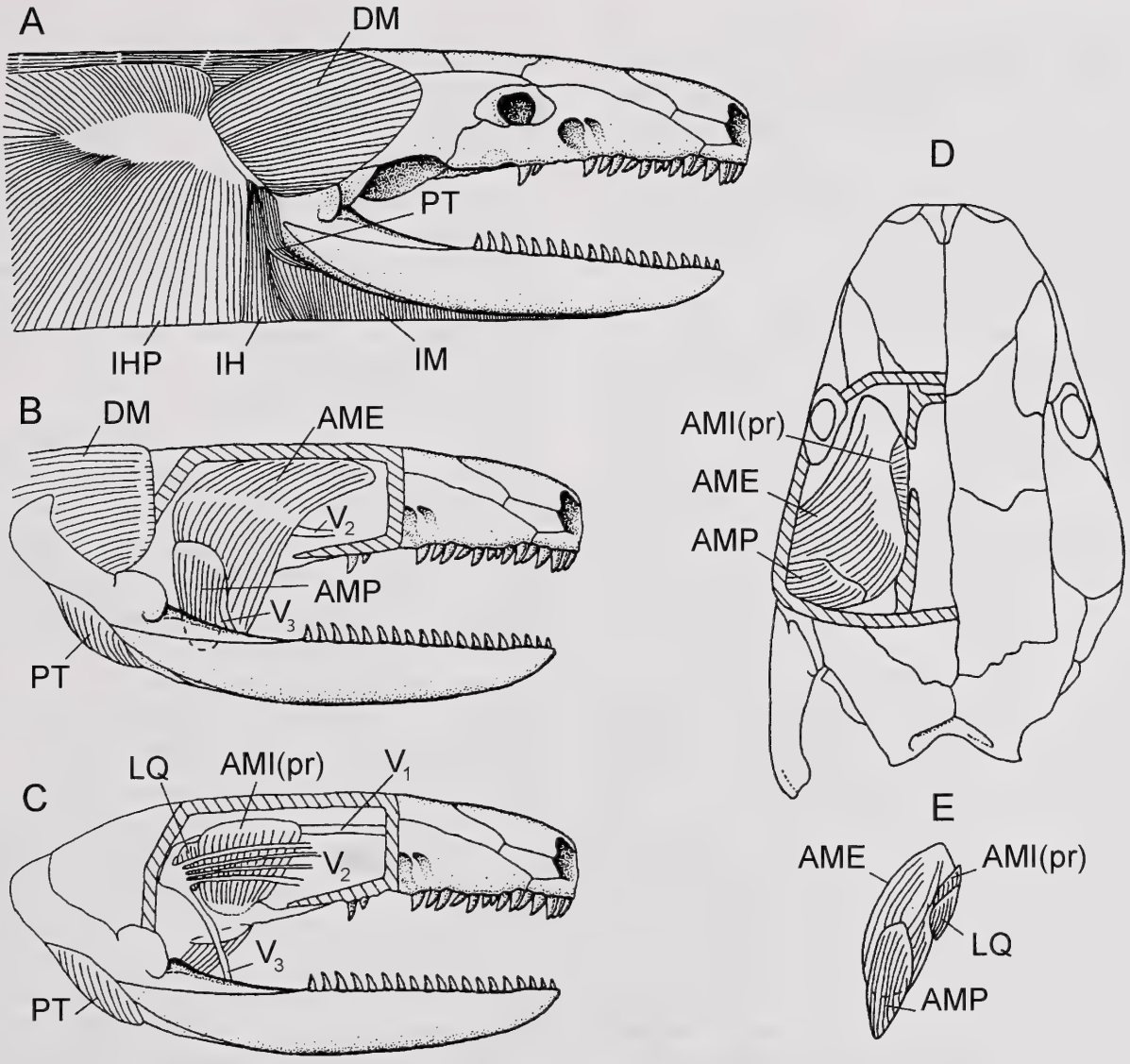

Figure 46. The jaw muscles in *Ichthyophis glutinosus*. (A) Lateral view of superficial muscles. (B, C) Lateral view of deep muscles, with the cranial vault resected (oblique hatching) to show origins within the adductor fossa. The muscles in plate B lie lateral to those in plate C. (D) Dorsal view of the adductor muscles with the cranial roof resected. (E) Isolated adductor muscles in posterior view.

(AMP) occupies the most posterior portion of the adductor chamber and is separated from the AME by V_3 (Fig. 46B, D). The AMP originates from two areas of the quadrate: the lateral surface of the pterygoid ramus and the medial surface of the palatine ramus. The insertion is within the mandibular fossa of the pseudoangular, which also transmits the mandibular ramus of V_3 and the mandibular artery.

In the upper portion of the adductor chamber, the adductor mandibulae internus (AMI) is separated from the AME by branches of V_2, and more ventrally, by connective tissue (Fig. 46C). The AMI originates somewhat ventral to the AME, from a more medial position on the underside of the skull roof. Most of the AMI joins the AME to share the same insertion in the mandibular fossa. A slip of the AMI (the levator quadrati, Fig. 46E), which arises from a more inferior position within the adductor chamber, is separated from the AMI by a large blood vessel accompanying the deep branch of V_1 and connective tissue. The slip converges to its attachment in a pit at the top of the pterygoid ramus of the quadrate.

In contrast to the other adductors, the pterygoideus is oriented more horizontally and is directed posteroventrally from its origin along the anterior margin of the adductor fossa. The muscle divides, with one part inserting on the anterior margin of the internal process of the mandible and the other extending across the ventral aspect of the retroarticular processes to insert on its lateral surface (Fig. 46C). The two divisions are separated by a robust ligament that connects the internal process and the pterygoid.

The interhyoideus posterior (IHP, Fig. 46A) is a large, fan-shaped muscle that arises from the dorsal and lateral aspects of the neck, and the ventral aspect of the gular and "cervical" regions. The fibers converge to insert on the retroarticular process.

A general assessment of the function of some of these muscles can be made from their fiber orientation, relative size, and mechanical advantage (lever arm length) with respect to the jaw joint. The three adductors (AME, AMP, and AMI) insert on the mandible in close proximity to the jaw joint and thus have less mechanical advantage than does the interhyoideus posterior that attaches to the long lever arm of the retroarticular process. Furthermore, the origin of the adductors is confined to a relatively small, enclosed adductor fossa, a common condition among extant gymnophionans (Fig. 6B, C); the adductor fossa in rhinatrematids is larger (Fig. 6D).

The diverging fiber directions of the interhyoideus posterior are evidence of multiple functions. Recruitment of the superior, dorsally directed fibers would raise the retroarticular process and thus initiate jaw opening. Conversely, the bulk of the muscle, with fibers directed ventrally or posteroventrally, would act to depress the retroarticular process and thus contribute to the uniquely caecilian jaw closure mechanism.

The contribution of the pterygoideus is less clear and could involve differential recruitment of its two divisions during the masticatory cycle. The oblique orientation of the division of the pterygoideus that inserts on the internal process likely contributes to jaw closure (a conventional function for the pterygoideus among tetrapods). The other division, which passes below the internal process of the pseudoangular and wraps around the ventral aspect of the retroarticular process, is of uncertain function. In some mandibles of *Eocaecilia micropodia,* a groove on the ventral aspect of the jaw below the internal process records the passage of this part of the muscle to the retroarticular process (Fig. 27D). The line of action of this part of the pterygoideus passes across the jaw joint (Fig. 46C); therefore, the fibers possess no lever arm for either jaw opening or closing. Two possibilities remain. This division could produce an anterodorsally directed compressive effect on the jaw joint. Such an action could contribute to joint stability and, in particular, serve as an antagonist to the posteroventrally directed force of the interhyoideus posterior during jaw closure. A second possibility is that this part of the pterygoideus everts (by longitudinal lateral rotation) the jaw upon opening; the depressor mandibulae would effect inversion upon jaw closing.

The similarities between *Eocaecilia micropodia* and Recent caecilians notwithstanding, the configuration of the stapes-quadrate, jaw joint, and internal process of the pseudoangular in *E. micropodia* is evidence of a divergence in masticatory mechanics. The geometric complexity of the articular surfaces borne by the quadrate and pseudoangular in gymnophionans (Fig. 29B, C), which provides structural stability, contrasts to the nearly vertically oriented, planar facets of *E. micropodia* (Fig. 29A). Unlike the modern caecilian jaw joint, in which the quadrate facets fit securely between condylar processes of the pseudoangular, no interlocking mechanism is present in *E. micropodia,* where the joint possesses no mechanical impediment to anteroposterior or dorsoventral translation. The dimensional differences in

the quadrate and pseudoangular facets are small, however. The evidence that pseudoangular facets are about 45% longer along an anteroposterior axis than facets on the stapes-quadrate supports an interpretation of slight protrusion upon jaw opening and retraction upon closing. The dentition of *E. micropodia*—with teeth that are numerous but very small—would seem suitable for apprehending only the smallest of prey, and propalinal jaw movements could well have been employed in ingestion. With a jaw joint of little intrinsic stability, the large size and dorsomedial orientation of the internal process might reflect the employment of the pterygoideus as a jaw protractor. The fusion of the stapes-quadrate and the unusual orientation of the jaw joint might represent a specialization to withstand the medially compressive forces generated by the interhyoideus posterior. In extant caecilians, the same medially compressive forces would be resisted by the obliquity of the complex interlocking of the quadrate and pseudoangular facets.

The Habitus of Eocaecilia micropodia. With the exception of aquatic species, gymnophionans are capable burrowers. Several anatomical features of *Eocaecilia micropodia* provide a basis for evaluating the degree to which this Early Jurassic caecilian can represent a stage in the evolution of gymnophionan fossoriality. In a review of tetrapod limblessness, Gans (1975) observed that the majority of limbless forms are shelterers or burrowers, the exception being snakes (although uropeltids among Serpentes are true burrowers). Lizards in which the limbs are reduced to various degrees (e.g., scincids, anguids, cordylids) are not effective burrowers but are principally shelterers in crevice-rich environments. Gans suggested that a universal correlate of limblessness is body elongation and that "limb reduction followed, and was probably produced by, selective pressure established after bodily elongation had occurred" (Gans, 1975: 465). However, in a review of limb reduction in squamates, Greer (1991: 167–171) noted that 22 of the 53 extant lineages that exhibit various degrees of limb reduction are not patently elongate, although he agreed that ". . . a gross reduction in the number of limb bones is always associated with an elongate body." Our estimate of the vertebral count in *E. micropodia* is suggestive of body elongation but does not demonstrate the feature unequivocally. The evidence that *E. micropodia* had undergone some reduction of the appendicular skeleton, however, is unambiguous (Jenkins and Walsh, 1993, table 1; Fig. 31). In addition to the retention of limbs, *E. micropodia* had not yet attained other characteristics that are likely to be related to the fossorial habits of gymnophionans. The mouth is not obviously subterminal as in gymnophionans. The orbits, although proportionately smaller than is typical for Paleozoic amphibians, are larger than those in gymnophionans in which the eyes are much reduced and in some taxa covered by bone. The atlanto-occipital joint of *E. micropodia* is relatively small compared with those of gymnophionans in which the robustness of the joint is integral to a burrowing style that employs head and "neck" movements.

We conclude that limited evidence favors the interpretation that *Eocaecilia micropodia* was probably not a burrower with the capabilities of Recent gymnophionans. The reduction in overall limb size and the apparent loss of two digits are features shared with various squamates that are either poor burrowers or sand swimmers or that shelter themselves in crevices and other cramped niches, such as dense vegetation (Gans, 1975). If this analogy is appropriate, then we might envision the habitus of these Early Jurassic caecilians as presenting substrate parameters sufficiently dense or spatially constraining that limb reduction was selectively advantageous. Thus, *E. micropodia* plausibly represents a stage in the evolution of gymnophionan burrowing but was probably not fossorial *per se*. The correlate of such a supposition

is that the relatively small head size, specializations of the masticatory apparatus, and other cranial features that characterize both *E. micropodia* and Recent gymnophionans and which are commonly assumed to be associated with the fossorial habits of gymnophionans, in fact arose during a stage in caecilian evolution before their entry into the subterranean world.

Zygokrotaphy and Stegokrotaphy. A persistently problematic issue in caecilian evolution is whether an open (zygokrotaphic) or closed (stegokrotaphic) skull roof in the temporal region is the primitive condition. Numerous studies, including those of DeBeer (1937), Goodrich (1930), Parsons and Williams (1963), and Wake and Hanken (1982), have supported the now prevalent view (reviewed by Wake, 2003) that one of the cranial specializations in living gymnophionans is secondary closure of the temporal fenestra, a derived condition most likely related to fossoriality. Bemis et al. (1983), in a functional study of feeding in *Dermophis mexicanus*, took no position on whether stegokrotaphy is primitive or derived. They suggested that the reduction in skull size that accompanied the development of burrowing habits places a constraint on the size of the adductor chamber and that the interhyoideus posterior/retroarticular process functions as a compensatory mechanism. Nussbaum (1983) observed that this novel mechanism is least well developed in rhinatrematids, which are relatively basal gymnophionans in which heads of the adductor mandibulae are exposed by a temporal fenestra. The temporal fenestrae of rhinatrematids and the inferred, secondarily closed fenestrae of more derived groups would thus be a feature shared with frogs and salamanders. The discovery of stegokrotaphy in an Early Jurassic caecilian, which is patently primitive in many cranial and postcranial characters, revived the alternative possibility that zygokrotaphy could be derived (Jenkins and Walsh, 1993). We reconsider this problem in light of this study.

Nussbaum (1983) presented four plausible lines of evidence in support of his interpretation that stegokrotaphy is secondary in caecilians. First, there are no temporal bones between the squamosal and parietal in living caecilians, whether they be zygo- or stegokrotaphic; he regarded their loss as more likely the result of temporal fenestration (displaced by expanded adductor muscles) than by in situ fusion. Alternatively, we note that fusion of adjacent cranial bones is known to have occurred extensively in caecilians (Wake, 2003; Wake and Hanken, 1982).

Second, Nussbaum (1983) noted that the arrangement of postorbital bones in stegokrotaphic caecilians differs from that in labyrinthodonts and considered this difference as evidence that a solid temporal region has been secondarily reconstructed. However, the architecture of the cranial vault in *Eocaecilia* is now known to include such elements as a postparietal, jugal, quadratojugal, and tabular (or supratemporal), all in comparable positions to those in the primitive tetrapod pattern.

Third, Nussbaum (1977, 1983) pointed out that the skulls of rhinatrematids (which are zygokrotaphic) and ichthyophiids (in which zygokrotaphy is incipiently developed) are primitive in the greatest number of features. Furthermore, the highly derived skulls of most caeciliids are stegokrotaphic, an exception being *Geotrypetes* (Wake, 2003). Alternatively, we note that the putatively primitive rhinatrematid, *Epicrionops*, exhibits a number of derived cranial features; these include loss of the pre- and postfrontals, encirclement of the orbital margin by the maxillopalatine, and specialization of the articulation between the squamosal and the lateral margin of the os basale. More primitive character states of these features are found in Ichthyophiidae and Uraeotyphlidae. Stegokrotaphy in *Eocaecilia* is associated with numerous primitive features of the skull and postcranial skeleton.

Finally, Nussbaum (1983: 551) suggested that the incomplete development of the interhyoideus jaw closure mechanism in

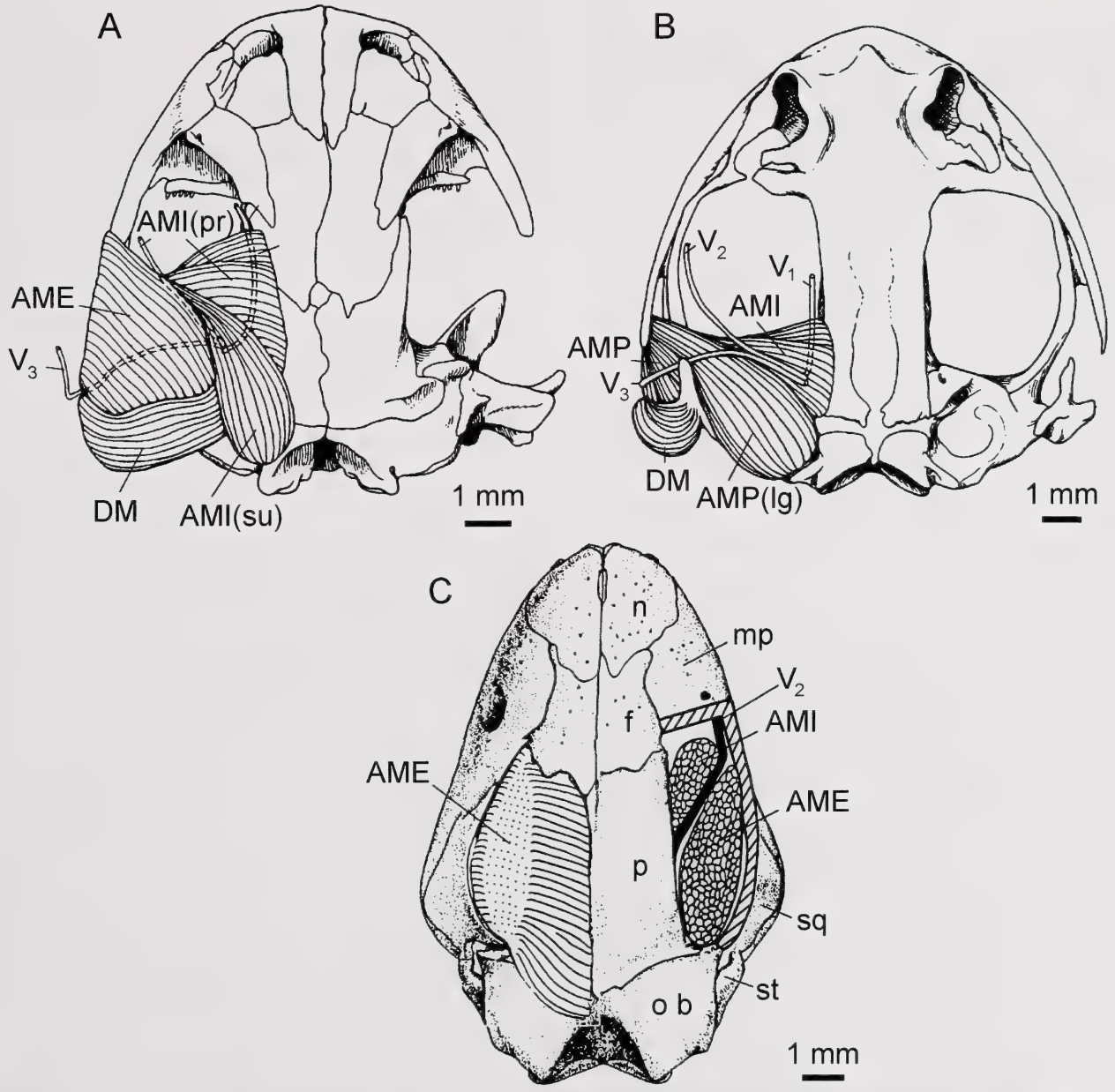

Figure 47. Dorsal view of adductor muscles in (A) a salamander, *Ambystoma maculatum*; (B) a frog, *Ascaphus truei*; and (C) a caecilian, *Epicrionops petersi*. A and B from Carroll and Holmes (1980, fig. 18); C reconstructed from sections (LSUMZ 27324).

rhinatrematids engendered a compensatory enlargement of "... the ancestral component [that] dominates by expansion of the *mam* [musculus adductor mandibulae] through a temporal fossa." Alternatively, we raise the possibility that rhinatrematids (and, to a lesser extent, other caecilians with incipient zygokrotaphy) might exhibit a secondary reduction of the contribution of the interhyoideus posterior to jaw closure and a commensurate increase in the size of the adductors.

Carroll and Holmes (1980) cited differences between frogs and salamanders in the arrangement of the adductor muscles in the temporal fenestra as evidence that the fenestrae themselves were independently derived. This comparison may now be extended to include a caecilian. The dominant muscle at the level of the temporal fenestra in salamanders is the external adductor (Fig. 47A), which is associated with loss of ossification between the maxilla and jaw suspension (Carroll and Holmes, 1980), whereas in frogs, the largest muscle is the posterior adductor (Fig.

47B). In *Epicrionops,* the dominant muscle is the external adductor (Fig. 47C). In each of these groups, different divisions of adductor mandibulae extend posteriorly over the back of the skull table and otic capsule: the long head of the posterior adductor in frogs, the superficial head of the internal adductor in salamanders, and the external adductor in *Epicrionops.* The divergent patterns of the occupation of the temporal opening in these three taxa might support the interpretation that the evolution of the openings occurred separately in the three groups. Alternatively, the relative size and positioning of the adductor divisions could reflect divergences in muscle function that developed subsequent to fenestration.

At present there is no certain basis for making a definitive decision on stegokrotaphy versus zygokrotaphy in caecilian phylogeny. That the stegokrotaphic condition is primitive for amphibians is undeniable—as is the fact that temporal fenestration and other modifications of the skull roof are known to have developed in other groups (e.g., Paleozoic lysorophid amphibians). The lingering questions are whether fenestration in caecilians had already been initiated in the common ancestor of lissamphibians, or whether the condition was acquired subsequently in the ancestors of some living caecilians. *Eocaecilia micropodia,* which is primitive in many aspects of the cranial and postcranial skeleton, supports the latter possibility.

Eocaecilia *as a Stage in Caecilian Phylogeny.* We concur with the phylogenetic hypotheses of Evans and Sigogneau-Russell (2001, fig. 8) and Trueb and Cloutier (1991, fig. 9) that *Eocaecilia micropodia* is a basal caecilian that lies outside the crown group Gymnophiona. This Jurassic form nonetheless has significant implications for our understanding of a previously unknown stage in caecilian evolution and diversity. *Eocaecilia micropodia* shares with extant gymnophionans such a substantial array of shared derived characters that there can be little doubt that the evolutionary transition to gymnophionans had largely taken place prior to the Early Jurassic. The most distinctive gymnophionan features of *Eocaecilia* are: a sulcus along the anteroinferior margin of the orbital rim that could be interpreted as a tentacular sulcus; an os basale representing consolidation of the supraoccipital, exoccipitals, basioccipital, basisphenoid, pleurosphenoid, and parasphenoid elements; an internal naris posterior to the premaxillary–maxillary suture and medial to the tooth rows on the vomer and palatine; enlarged nasal capsules that lie between the sphenethmoid and rostral margin of the skull; an olfactory eminence on the vomer; a lower jaw comprising a pseudodentary and pseudoangular that meet along an elongate, oblique suture; and an internal process of the pseudoangular. Internal processes of the pedicles, which serve to anchor tissue suspending the spinal cord, were first discovered in *E. micropodia* and subsequently found in some gymnophione taxa. On the basis of limited evidence, *Eocaecilia* appears to exhibit an elongation of the body comparable to that in primitive extant gymnophionans, but a detailed comparison cannot be made because of uncertainty over the precise number of vertebrae.

In contrast to the foregoing gymnophionan synapomorphies, *Eocaecilia* also presents primitive or transitional features, or both, that might be expected in forms representing a transition to a highly specialized life style. The retention of jugal, quadratojugal, ?tabular, and postparietal bones is primitive. The presence of intercentra and limbs is also primitive, but the reduction in the relative size of the limbs would appear to be transitional toward the gymnophionan condition.

The discovery of an operculum in *Eocaecilia micropodia* is novel confirmatory evidence that the opercular apparatus is a synapomorphy of Lissamphibia. The apparent absence of an operculum in extant gymnophionans (at least as a separate

element) is best explained by the related loss of the shoulder girdle and muscular link between the girdle and operculum. The accessory ear ossicle described by Carroll and Gaskill (1978: 163, fig. 113) in *Rhynchonkos* and other microsaurs is consistently suspended above the stem of the stapes; in shape and position this ossicle appears to differ from the operculum of *Eocaecilia,* which is oval and, in one specimen at least, is preserved in close association with the fenestra ovalis. In contrast to the operculum, the presence of pedicellate teeth in a Jurassic caecilian is entirely expected. This dental specialization, once widely recognized as a lissamphibian synapomorphy, is now known to occur in two Paleozoic amphibians—*Doleserpeton* (Bolt, 1969, 1991) and *Apateon* (Schoch and Carroll, 2003)—which have been interpreted to be sister taxa of frogs and salamanders, respectively.

With an admixture of primitive, transitional, and demonstrably gymnophionan features, *Eocaecilia* appears even more chimeric in possessing an array of specializations that, on present knowledge, are autapomorphic. Many of these features present a perplexing challenge to functional interpretation, for no structural comparability is to be found among living or potentially antecedent forms. The internal process of the lower jaw is very robust, and projects into the adductor chamber. The obliquely oriented, more or less planar jaw joint would appear to provide little stability, and is thus structurally and functionally unlike that known in any other caecilian. The stapes-quadrate is also unique.

Although our knowledge of caecilian evolution and diversity now extends into the Early Jurassic, *Eocaecilia micropodia* does not provide sufficient evidence to securely recognize the origin of gymnophionans among known Paleozoic amphibians, or even contribute substantially to the unresolved issue of liassamphibian monophyly. Carroll and Currie (1975) proposed microsaurs as possible caecilian ancestors, but their hypothesis has been criticized by Bolt (1991), among others, and is not widely accepted. Nonetheless, the third author of this monograph persists in this viewpoint (Carroll, 2000: 1410), from which the remaining authors must demur. We therefore address the list of putative synapomorphies that have been proposed as uniting *Eocaecilia* and the tuditanomorph microsaur *Rhynchonkos* [*Goniorhynchus*], many of which have already been critiqued by Bolt (1991).

1. "far anterior jaw articulation." The relative position of the jaw articulation in the reconstructed skulls of *Rhynchonkos* (Carroll, 2000, fig. 2A, B; Carroll and Gaskill, 1978, figs. 63, 64) is not certainly comparably displaced as in *Eocaecilia.* The central issue is the position of the jaw joint relative to the occiput. To the degree that the central third of the occiput is protracted posteriorly relative to the two lateral thirds, the jaw joint will seem anteriorly displaced. The senior author examined the original material of *Rhynchonkos stovalli* (FMNH-UR 1039 and 1040), and both specimens are deformed and crushed (as shown in Carroll and Gaskill, 1978, figs. 63A, 64, top row), particularly in the occipital region. Not surprisingly, Carroll and Gaskill's two reconstructions (1978, figs. 63B, 64, bottom row) are slightly different. Thus, with the reliability of the reconstructions uncertain, the relative position of the jaw joint in *Rhynchonkos* is moot.

2. "conspicuous retroarticular process." Without attempting to define conspicuous as a quantifiable morphological term, we note that the retroarticular process of *Rhynchonkos* is short (estimated at 5–6% of jaw length) relative to that in *Eocaecilia* (17–18% of jaw length). Retroarticular processes occur widely throughout temnospondyls and are not uniquely shared by *Rhynchonkos* and *Eocaecilia.* In addition to *Rhynchonkos,* retroarticular processes in microsaurs are also found in ostodolepids and some gymnarthrids (Carroll and Gaskill, 1978).

3. "loss of intertemporal and supratemporal." This character has previously been

criticized by Bolt (1991) who pointed out that absence of the intertemporal and supratemporal does not constitute a unique synapomorphy with any of the lissamphibian orders. "The intertemporal is absent in numerous fossil amphibian groups, and the absence of both intertemporal and supratemporal is shared at least with advanced aistopods, lysorophoids and adelogyrinids . . ." (Bolt, 1991: 208–209).

4. "medial rows of teeth on the palate and lower jaw." Bolt (1991: 209) observed that "Many fossil amphibians have a row of palatal teeth disposed like that of *Rhynchonkos*—this character has evolved independently a number of times, on almost any hypothesis of amphibian relationships." As Bolt (1991: 210) further pointed out, *Rhynchonkos* is hardly unique in the possession of an internal row of mandibular teeth, which occurs in various temnospondyls (Jupp and Warren, 1986), including *Colosteus* (Hook, 1983).

5. "closely integrated posterior portion of the braincase." Without attempting to define close integration, we note that Bolt (1991: 209) previously rejected Carroll and Currie's (1975: 237) use of the character of "an extensive pleurosphenoid [that] joins the otico-occipital portion of the braincase with the sphenethmoid." Lateral ossification of the braincase between the otic capsules and sphenethmoid is not unique to microsaurs.

6. "closure of the region anterior to the opening of the Vth nerve." Enclosure of the exit of the trigeminal nerve by a bony pleurosphenoid is simply an expression of the degree of ossification of the braincase and is not uniquely shared by *Rhynchonkos* and caecilians.

7. "holospondylous centra." Holospondylous vertebrae are characteristic of lissamphibians and lepospondyls generally and are not shared just with microsaurs. The general trend of vertebral evolution among Paleozoic amphibians was a reduction of one of two circumnotochordal elements (intercentrum, pleurocentrum) in favor of establishing the other as the dominant, or sole, element.

8. "double occipital condyle." Paired occipital condyles occur in many derived temnospondyls and other lissamphibian groups and are not uniquely shared by *Rhynchonkos* (and microsaurs) and *Eocaecilia* (and gymnophionans).

9. "elongation of the [vertebral] column" and

10. "reduction of limbs." Lengthening of the body through an increase in vertebral number has occurred repeatedly and independently in amphibian evolution—salamanders, lepospondyls, and aistopods being several examples. Likewise, limb reduction or loss has developed convergently in various aquatic or burrowing amphibians. Both characters denote a general resemblance, but neither is uniquely shared by *Rhynchonkos* (and microsaurs) and *Eocaecilia* (and gymnophionans).

11. "a more general similarity is small size." Small size is indeed a general similarity, but diminutive taxa are found across many amphibian groups. Size is more likely a consequence of convergence and provides no persuasive indicator of relationship between microsaurs and *Eocaecilia*.

We thus conclude, with our third author dissenting, that on available evidence, *Eocaecilia* and gymnophionans have no demonstrable relationship to Microsauria. The authors do concur that a substantial morphological and temporal gap still intervenes in the identification of the origins of caecilians, and in fact we might not even be in possession, among all the Paleozoic taxa now known, of the fossil record of caecilian origins. Although Bolt and Lombard (1985; see also Lombard and Bolt, 1988) have produced the most credible evidence yet of an anuran relationship to temnospondyls, and Schoch and Carroll (2003) have identified developmental similarities between branchiosaurids and salamanders, the concept of Lissamphibia still remains at best a crown group taxon, without a securely rooted stem in the Paleozoic.

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APPENDIX:
A List of *Eocaecilia micropodia* Specimens

SPECIMENS ACCESSIONED IN THE MUSEUM OF COMPARATIVE ZOOLOGY

MCZ 9011	anterior two-thirds of skull and jaws
MCZ 9015	crushed skull and jaws; a second skull crushed and disarticulated, including tooth crowns
MCZ 9095	disarticulated jaws, fragmentary vertebrae
MCZ 9152	left lower jaw, vertebra
MCZ 9156	crushed and disarticulated skull
MCZ 9158	right lower jaw mounted on SEM disc, partial left lower jaw, and ?skull fragments
MCZ 9163	crushed skull and jaw, vertebrae and

	various limb bones including complete humerus (mounted on SEM disc) and ulna
MCZ 9166	incomplete mandibles and postcranial bones; proximal humerus mounted on SEM disc
MCZ 9167	partial skull roof with otic region, atlas, partial lower jaw, distal humerus, proximal ulna
MCZ 9169	block A: articulated vertebral series with shoulder girdle and forelimb elements, prepared and mounted on an SEM disc; block B: disarticulated vertebral series including caudals; blocks C, D: articulated vertebral series with crushed skull and jaws; isolated teeth mounted on SEM discs
MCZ 9171	proximal humerus, partial jaws, atlas, vertebrae, scapulocoracoid, and crushed, disarticulated skull
MCZ 9173	fragmentary vertebra
MCZ 9231	atlas and other fragmentary vertebrae, partial jaw
MCZ 9233	disarticulated jaws
MCZ 9235	crushed, disarticulated skull with stapes-quadrate, jaw, and vertebrae
MCZ 9237	crushed skull and mandible, humeri, scapulocoracoid, ?ulna, and associated tibia and fibula with two tarsals
MCZ 9238	scapulocoracoid, ulna, and proximal humerus mounted on SEM disc; vertebrae
MCZ 9241	fragmentary jaw and vertebrae
MCZ 9242	disarticulated skull and jaws, isolated pterygoid, vertebrae, and associated radius and ulna mounted on SEM disc

SPECIMENS ACCESSIONED IN THE MUSEUM OF NORTHERN ARIZONA

MNA V8053	left lower jaw and vertebra
MNA V8054	vertebrae, stapes-quadrate, fragmentary right jaw, and ulna; posterior part of jaw and stapes-quadrate prepared
MNA V8055	several series of vertebrae on different blocks: an articulated posterior dorsal series and an incomplete caudal series; tibia, tarsals, metatarsals
MNA V8056	incomplete skull and jaws, scapulocoracoid on SEM disc, distal humerus, proximal radius and ulna, and fragmentary pedal elements
MNA V8057	vertebrae and ribs
MNA V8058	partial lower jaw
MNA V8059	incomplete skull and jaws with associated postcranial bones
MNA V8060	disarticulated skull and jaws and vertebrae
MNA V8062	articulated posterior dorsal vertebrae, ?sacrals, and caudal vertebrae, crushed skull and jaws, hindlimb elements including phalanges; right femur mounted on SEM disc
MNA V8063	otic capsule with braincase
MNA V8064	vertebrae, right scapulocoracoid (in medial view)
MNA V8065	partial skull roof with otic region, atlas, partial lower jaw, distal humerus, proximal ulna, and partial scapulocoracoid
MNA V8066	[holotype] skull and jaws with associated atlas and postatlantal vertebrae
MNA V8067	articulated vertebral series
MNA V8068	mandible and distal humerus
MNA V8069	vertebrae
MNA V8070	disarticulated skull, mandible, and stapes
MNA V0871	fragmentary skull showing palate, side of os basale, and ethmoid portion of braincase; vertebrae
MNA V8072	fragmentary lower jaw and stapes
MNA V8073	vertebrae and limb elements, including fragmentary pedal bones
MNA V9346	incomplete skull and jaws originally associated with MNA V8059

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Bulletin OF THE
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The *Cerion* (Mollusca: Gastropoda: Pulmonata: Cerionidae) Taxa of Charles Johnson Maynard and Their Type Specimens

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THE *CERION* (MOLLUSCA: GASTROPODA: PULMONATA: CERIONIDAE) TAXA OF CHARLES JOHNSON MAYNARD AND THEIR TYPE SPECIMENS

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ABSTRACT. Charles Johnson Maynard (1845–1929) was a self-educated naturalist, teacher, and dealer in natural history specimens and materials who conducted extensive field work throughout Florida, the Bahamas, and the Cayman Islands. He published prolifically on the fauna, flora, and anthropology of these areas. His publications included descriptions of 248 of the 587 validly proposed species-level taxa within Cerionidae, a family of terrestrial gastropods endemic to the islands of the tropical western Atlantic. After his death, his collection of Cerionidae was purchased jointly by the Museum of Comparative Zoology (MCZ) and the United States National Museum, with the presumed primary types remaining at the MCZ and the remainder of the collection divided between these two museums and a few other institutions. In this work, we provide 1) a revised collation of Maynard's publications dealing with Cerionidae, 2) a chronological listing of species-level taxa proposed in these works, 3) a determination of the number and status of name-bearing type specimens for each taxon within the context of the most recent edition of the International Code of Zoological Nomenclature, and 4) when necessary, the selection of a lectotype (for 185 taxa) or the designation of a neotype (for eight taxa) from among specimens in these museums to restrict the name-bearing type for each taxon to a single specimen, which is illustrated. Type material could not be located for three of the 248 species-level taxa proposed by Maynard. In these instances, neotypes are proposed to make these three taxa objective junior synonyms of other taxa. Strict application of the International Code of Zoological Nomenclature contradicts the authorship, publication date, and type status of name-bearing types for a significant number of Maynard's taxa that had been previously reported in the literature.

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INTRODUCTION

The family Cerionidae comprises a group of terrestrial pulmonate gastropods that are endemic to the tropical western Atlantic, ranging from southern Florida throughout the Bahamas, Greater Antilles, Cayman Islands, western Virgin Islands, and the Dutch Antilles, but are absent in Jamaica, the Lesser Antilles, and coastal Central and South America. These snails are halophilic, occurring on terrestrial vegetation, generally within 100 m of the shore, but occasionally 1 km or more from the sea, presumably in areas where salt spray can reach them from one or more directions (Clench, 1957: 121). Cerionid snails generally occur in dense but patchy populations, often with 10,000 or more individuals. They can be conspicuously abundant when living on open vegetation and less so when living in leaf litter. Although individual populations tend to be fairly uniform in the size and morphology of their shells, size, shape, color, and internal as well as external sculpture of the shell vary enormously among populations. Such variation is evident not only throughout the range of Cerionidae, but even among neighboring populations separated by less than 100 m. This lavish yet geographically circumscribed diversity has led to an extensive body of literature dealing with cerionids. Much of the early work was primarily taxonomic and focused on parsing the various phenotypes among roughly 600 nominal species and nearly two dozen genus-level taxa. More recent research,

particularly the work of Mayr, Gould, Woodruff, and Goodfriend, as well as their students and collaborators (see Woodruff, 1978, for an overview), addressed more basic biological questions: among them, the origins as well as the geographic and temporal stability of morphological and genetic diversity and the dynamics of hybrid zones and biogeographic patterns, both Holocene and Recent. Yet, as noted by Woodruff (1978: 224), "the evolutionary importance of these remarkable animals has been buried under an all but impenetrable taxonomic thicket."

Much of the breadth and a substantial amount of the impenetrability of this "taxonomic thicket" can be attributed to the work of Charles Johnson Maynard (1845–1929), who published 248 of the 587 validly proposed species-level taxa (excluding obvious typographical errors), and seven of the 23 genus-level taxa within Cerionidae. Maynard was a self-educated naturalist and teacher who conducted extensive field work throughout Florida, the Bahamas, and the Cayman Islands (Abele, 2002; French, 1930; Johnson, 1930; Townsend, 1930; Turner, 1957). His bibliography consists of 277 publications (Batchelder, 1951), the overwhelming majority on birds, but includes works on butterflies, sponges, land snails, and many other areas of natural history and anthropology. Batchelder (1951: 227) pointed out that many of Maynard's publications, including all of his work on Cerionidae, were "not only the work of his active mind but of his own hands. He took pride in setting the type, making wood-cuts, drawing lithographs, and doing the press work."

Maynard's publications were printed in limited numbers and most are very rare. For example, the prospectus on the inside front covers of each of the 12 parts of his *Contributions to the History of the Cerionidae with Descriptions of Many New Species and Notes on Evolution in Birds and Plants* (1919–26; hereafter *Contributions to the History of the Cerionidae*) states, "The edition will consist of 150 copies." Maynard's writings on the Cerionidae were confined to eight publications, several of which appeared in multiple parts (Table 1). Six of these publications contain descriptions of new taxa, and a seventh contains a nomen nudum. One is an advertisement.

Although Maynard's publications are rare, specimens of the majority of his taxa are not. In his undated sales catalog, Maynard (1924b?) mentioned having 200,000 specimens of *Cerion,* whereas the supplement to this catalog noted that an additional 44,000 specimens, representing 30 species, were collected in 1924. Nearly all of Maynard's species descriptions mention the number of specimens examined. In his description of *Strophia extensa,* as an extreme example, Maynard (1924c: 2–3) commented that 23,000 specimens were collected, of which only about 3,000 were living.

Shortly after Maynard's death (October 15, 1929), his daughter offered his large collection of *Cerion* for sale to the Museum of Collective Zoology (MCZ). Turner (1957: 151) reported that, "As the collection was so large, and the specimens so numerous, it was decided to buy it jointly with the United States National Museum [USNM, now the National Museum of Natural History, Smithsonian Institution] for $500. The collection was divided equally between the two institutions, with the holotypes being retained at the MCZ. A few duplicate sets of the larger series of Maynard's types were sold to various institutions, so that much of Maynard's type material is now well distributed." Records at the MCZ (Mollusk Department Accession file 766) indicate that 475 lots of "mostly cerions from the Maynard collection, including all of his species" were purchased by Dr. T. Barbour for the Museum and were received in the Mollusk Department in October 1931. These were assigned catalog numbers ranging from MCZ 76001 to 76475. Specimens with these catalog numbers were in Maynard's collection at the time of his death. Com-

menting on the condition of the collection, Turner (1957: 151) wrote "the collection, at the time it was sold, was in rather sad shape, for the cabinet drawers had warped and once pulled open could not be closed. The top drawers of the cabinets became a parade ground for pigeons, and their droppings cemented the shells together in a solid mass! After transferring the collection in its original drawers to the MCZ, each lot was sorted, cleaned and properly labeled—a truly gigantic task."

Because Maynard was a dealer and collector who for decades sold or exchanged specimens to support his research and expeditions, an unquantified amount of type material was also distributed during his lifetime. A series of cerions was donated by Maynard to the MCZ in 1895 and was catalogued with the numbers MCZ 10242 to 10360. Correspondence and invoices in the Smithsonian Archives indicate that Dr. Paul Bartsch purchased for the National Museum of Natural History specimens representing 121 of Maynard's species "from their type localities" in 1923 (USNM 359387–359518), and an additional 57 specimens in 1925. Another series of Maynard's cerion specimens, originally in the collections of the Boston Society of Natural History, was transferred to the MCZ in February 1930 and bear the catalog numbers MCZ 39713–39719. Although many of Maynard's taxa are represented in museum collections, particularly in the eastern United States, the type status of many, if not most, of these specimens was undetermined or incorrectly labeled at the time of this writing.

Although Turner (1957: 151) reported that the holotypes of Maynard's taxa were retained at the MCZ, it is far from clear how many and which of Maynard's taxa are based on holotypes and which on syntypes. If application of the International Code of Zoological Nomenclature (ICZN) is restricted to the descriptions of individual species, one conclusion can be reached. If other portions of the original publication are considered, this conclusion could be contradicted. By way of example, the original description of *Strophia scripta* Maynard, 1896 (p. 4), provided a detailed description that lists "size of type, 1.30 by .47" and identifies the illustration of a single specimen as "fig. 3, front, fig. 4, side view of type." According to Article 73.1.1 (ICZN, 1999: 79), this specimen would be the holotype. However, earlier in the same publication, Maynard (1896: 1) states, "The first portion of the present installment of this monograph is based upon specimens belonging to the MCZ which I have been permitted to examine. . . . I have returned the types figured to the Museum, but have retained a set of co-types in my own collection." This indicates that the figured specimen returned to the MCZ and the specimen retained by Maynard for his own collection are syntypes because they can be considered expressly designated as such in the original publication (Article 73.2.1, ICZN, 1999: 81).

Most of the taxon descriptions published in Maynard's first work on the Cerionidae, the *Monograph of the Genus* Strophia, *a Group of Tropical and Sub-Tropical Land Shells* that appeared in seven issues of the *Contributions to Science* (1889–96), were exemplary for the period. Each included a detailed description and illustrations (usually with two views), provided dimensions of the "type" or "types," as well as of the largest and smallest specimens, and had sections with observations on variation within the taxon and on its distribution and habitats.

In contrast, taxonomic descriptions in most subsequent publications (e.g., Maynard, 1913a,b,c, 1919–26 [*Contributions to the History of the Cerionidae*], 1924b?,c; Maynard and Clapp, 1914, 1915) were very brief and written in telegraphic style. Some were later supplemented with more detailed descriptions of the shell and anatomy (Maynard, 1924a, 1925, 1926). Each intended taxonomic description typically included a measurement and gave the number of specimens examined but did not contain any version of the

TABLE 1. PUBLICATIONS BY CHARLES JOHNSON MAYNARD CONTAINING ARTICLES ON CERIONIDAE.

Maynard, C. J. 1889–96. Monograph of the Genus Strophia, a group of tropical and sub-tropical land shells. Contributions to Science, **1**(1, April 1889): 1–29, pls. 1–2; **1**(2, July 1889): 68–79, pl. 7; **1**(3, October 1889): 125–135, pl. 16; **1**(4, January 1890 [dated "January, 1889" on page 1]): 188–197; **2**(1 [July 1893 on cover, November 1893 on page 1]): 1–48; **2**(2 [November 1894 on cover]): 49–104; **2**(3 [December 1894 on cover]): 105–152; **2**(4 [December 1894 on cover]): 153–200; **3**(1, March 1896): 1–40, pls. 1–7. (Privately published, Newtonville, Massachusetts)

Maynard, C. J. 1913. Descriptions of some species of the family Cerionidae. Records of Walks and Talks with Nature. Appendix to Volume 5: 177–200 (illustrations on paper covers; pp. 177–182 are dated January 1913; pp. 183–200, February 1913. Footnote on p. 186: "Pages 183–186 were issued Feb. 1, 1913." Footnote on p. 199: "Pages 187–199 were issued Feb. 9, 1913." Text is complete on p. 199. Page 200 contains figures of three species reproduced from *Contributions to Science*). (Privately published, West Newton, Massachusetts)

Maynard, C. J. 1914. A species of land shell of the family Cerionidae redescribed. Records of Walks and Talks with Nature. Appendix to Volume 6: 177–179 [illustrations on paper covers]. [Dated May 1914 at top of each page, but footnote on p. 179 states "Actual date of publication of this sheet, Aug 18, 1914."] (Privately published, Newtonville, Massachusetts)

Maynard, C. J., and N. A. Clapp. 1914–15. Descriptions of new Strophias. Records of Walks and Talks with Nature. Appendix to Volume 6: 180 [August 18, 1914], 179 bis, 180 bis, 181, 182 [February 8, 1915]. [Page 180 has same date as Maynard, 1914; footnote on p. 182 states, "Actual date of publication, Feb. 8, 1915."] (Privately published, Newtonville, Massachusetts)

Maynard, C. J. 1919. A New Book on Evolution. Contributions to the History of Cerionidae. 4 unnumbered pp. (Privately published, Newtonville, Massachusetts)

Note: This is a four-page advertisement for the *Contributions to the History of the Cerionidae* [see below] that provided a brief description of the intended work, which was to contain "upward of 400 pages, and over 20 plates of shells, birds, etc" and be limited to 150 copies. Versions with either plain or hand-colored plates were advertised. This advertisement was bound within the covers of Number 1 of *Contributions to the History of the Cerionidae* in the ANSP copy, with a Library Stamp dated October 22, 1919. Batchelder (1951: 256) noted, "Issued first perhaps in 1921, reprinted, most of it verbatim, but with some changes, in 1924."

Maynard, C. J. 1919–26. Contributions to the history of the Cerionidae with descriptions of many new species and notes on evolution in birds and plants. Records of Walks and Talks with Nature. Appendix to Volume 10. **1**[October 16, 1919]: 1–24, pls. 5, 6 [illustrations on paper covers]; **2**[November 6, 1919]: 25–52, pls. 7, 8 [illustrations on paper covers]; **3**[December 31, 1919]: 53–68, pls. 9, 10 [illustrations of paper covers]; **4**[February 29, 1920]: 69–80, pls. 10*, 11 [illustrations on paper covers]; **5**[April 8, 1920]: 81–92, pls. 12, 13 [illustrations on paper covers]; **6**[July 10, 1920]: 93–110, pls. 14–19 [illustrations on paper covers]; **7**[September 30, 1920]: 111–126, pls. 1–4, 20–25 [illustrations on paper covers]; **8**[May 2, 1921]: 127–138, pls. 26–33 [illustrations on paper covers]; **9**[July 15, 1921]: 139–154, pls. 34–37 [illustrations on paper covers]; **10**[October 25, 1924]: 155–170, pls. 38–39 [illustrations on paper covers]; **11**[July 18, 1925]: 171–194, pls. 40–41 [illustrations on paper covers]; **12**[March (10 printed, overwritten in ink to 24) 1926]: 195–218, pls. 42–43 [illustrations on paper covers]. (Privately published, Newtonville, Massachusetts)

Note: Collations and dates of individual parts of this work are based on copies in the libraries of the Smithsonian Institution and the Academy of Natural Sciences of Philadelphia, which were bound as issued. The dates and the apportionment of pages, especially of plates to the individual numbers, differ considerably from the collation given in Batchelder (1951: 254–256), which, like the copies in the libraries of the MCZ and Mr. Richard Goldberg, have the plates in numerical order. The collation of this work in the library of the Field Museum of Natural history differs in that 1) pages 49–52 are bound with number 3 instead of number 2; 2) number 3 is dated (in pencil) December 4 instead of December 31; 3) plates 40 and 41 are bound between the back cover of number 10 and the front cover of number 11, rather than within the covers of number 11.

Publication dates are based on:

"Number 1 Published Oct. 6 1919" printed on front cover.

* "Number 2 Published Nov. 6 1919" printed on front cover.

* "Number **3** Published Dec. **31** 1919" printed on front cover but numbers in **bold** handwritten in ink.

TABLE 1. CONTINUED.

"Number 4 Date of issue on last page." printed on front cover. Footnote on p. 80, "No. 4. Pages 69–80, inclusive. issued Feb. 29, 1920."
"Number 5 Date of issue on last page." printed on front cover. Footnote on p. 92, "No. 5. Pages 81–92, inclusive. issued April 8, 1920."
"Number 6 Date of issue on last page." printed on front cover. Footnote on p. 110, "No. 6. Pages 93–110, inclusive. issued July 10, 1920."
"Number 7 Date of issue on last page." printed on front cover. Footnote on p. 126, "No. 7. Pages 111–126, inclusive. issued Sept. 30, 1920."
"Number 8 Date of issue on last page." printed on front cover. Footnote on p. 138, "No. 8. Pages 127–138, inclusive. Issued May 2, 1921."
"Number 9 Date of issue on last page." printed on front cover. Footnote on p. 154, "No. 9. Pages 139–154, inclusive. issued July 15, 1921."
"Number 10 Date of issue on last page." printed on front cover. Footnote on p. 170, "No. 10. Pages 155–170, inclusive. issued Oct. 25, 1924."
"Number 11 Date of issue on last page." printed on front cover. Footnote on p. 194, "No. 11. Pages 171–194, inclusive. Issued July 18, 1925."
"Number 12 Date of issue on last page." printed on front cover. Footnote on p. 218, "No. 12. Pages 195–218, inclusive. Issued March 10 [overwritten in ink to 24], 1926."

Maynard, C. J. [Undated, referred to herein as 1924b?]. Catalogue of Specimens of the Family Cerionidae for Sale by Charles J. Maynard Containing Many New Species. Paper cover and 8 unnumbered pages. (Privately published, Newtonville, Massachusetts)

Note: Batchelder (1951: 256) listed 1920 as the date for this work, whereas Clench (1957: 169) cited a six-page catalog with identical title as published in 1924. Maynard began advertising specimens and publications in *The Nautilus,* beginning in July 1920 and continued until October 1929 (volume 34, number 1, through volume 43, number 2), the advertisements appearing at the top of the inside front cover. Beginning July 1921 and continuing until Maynard's death (October 15, 1929), these advertisements offered a "Catalog of Cerion for sale now ready, over 100 species." The inside front paper cover of the Catalog in the Smithsonian Institution's library lists "Appendix to Records Vol. X, 1921," and several taxa described in 1921 are offered for sale in this catalogue. Also listed [page 3] is *Strophiops albicostata,* the description of which appears in the supplement to this catalog (dated December 10, 1924). These data suggest that the catalog first appeared on or before July 1921 but that it might have undergone periodic revision and updating, the last appearing on or before December 10, 1924. The copy in the Academy of Natural Sciences Library is hand dated "1921," but the Library Stamp reads January 31, 1929.

Maynard, C. J. 1924 [10 December]. Supplement to Sale Catalogue of Cerionidae with Descriptions of New Species Collected in the Bahama Islands in Summer of 1924. pp. 1–6. [Footnote on p. 6 "Issued December 10, 1924] (Privately published, Newtonville, Massachusetts)

* Asterisk denotes a date different from that cited by Batchelder (1951: 254).

word "type" in the description or in figure captions for those taxa that were illustrated. International Code of Zoological Nomenclature Article 73.2 (1999: 81) states that, "for a nominal species-group taxon established before 2000 all specimens of the type series are automatically syntypes if neither a holotype nor a lectotype has been fixed." Thus, most of Maynard's taxa published after 1896, including the taxa of Maynard and Clapp, can be considered as being typified by multiple syntypes (23,000 syntypes in the case of *Strophia extensa* Maynard, 1924; see above).

In the preamble to the species descriptions published in *Contributions to the History of the Cerionidae* under the heading "Typical Specimens," Maynard wrote,

> It has long been the custom with naturalists when describing new species to select some individual specimen that as nearly as possible combines all of the characters which are possessed by the species of which it is a member. This specimen is called a type. As will be seen, however, by the previous remarks and the matter which follows, that groups occur in all species composed of members which have similar characters. From some one of these groups the type must be selected. This is usually selected in the species described in this volume, from the group that has the largest number of specimens. This group I have called typical. (Maynard, 1919b: 43–44)

This indicates that Maynard understood the concept of type specimen and defined it explicitly. Maynard based his taxonomic descriptions on characteristics of populations, then selected as "type" an individual that "as nearly as possible combines all of the characters possessed by the species of which it is a member." This differs conceptually from the definition of Holotype, which is "the single specimen upon which a new nominal species group taxon is based" (Article 73.1, ICZN, 1999: 79).

Maynard's statement that "this [the type] is usually selected in the species described in this volume" not only excludes species not described in that volume (i.e., Maynard, 1913a, b, c, 1924b, c; Maynard and Clapp, 1914, 1915) but does not specify for which of the species in Maynard (1919–26) such specimens were selected.

Even with no mention of the term "type" in the original descriptions, many of the specimens now in the collections of the MCZ that are derived from the Maynard collection are labeled "Holotype" and are accompanied by a slip of paper, apparently in Maynard's handwriting, that includes the term "type." These labels also contain the plate and figure numbers for the illustrations of the taxon in Maynard (1919–26) in the same handwriting and the same ink, suggesting that the slips were written at the time of preparation of the plates for this work. Such labels can be construed as evidence that Maynard considered these specimens to be the types of their respective taxa, some of which had been published years or decades earlier than their illustrations. However, it is not possible to interpret them as holotype designations within the Code, which states that "the holotype of a new nominal species-group taxon can only be fixed in the original publication by the original author" (Article 73.1.3, ICZN, 1999: 79).

In the vast majority of cases, these "type" labels accompany a single specimen, but in over a dozen cases, they accompany a lot containing multiple specimens. Given the condition of the collection at the time of Maynard's death (see above; Turner, 1957: 151), it is entirely possible that specimens or labels moved within the drawers. When such specimens, or one of such specimens, can be reasonably construed as approximating the published measurements or, for taxa that are illustrated, the original illustration, even though neither are associated with the term "type" within the publication, these specimens are designated as the lectotypes for their respective species-level taxa herein.

Many researchers have conjectured that perhaps only 10–20% of the species-level taxa within Cerionidae will eventually be found to represent valid species (e.g., Clench, 1957: 121; Turner, 1957: 152; Woodruff, 1978: 235). The determination of whether the nomina proposed by Maynard represent valid species, subspecies, demes, or distinctive combinations of alleles is beyond the scope of this work. Rather, our objective here is to enumerate chronologically and in order of publication all of the species-level taxa within the family Cerionidae that were validly proposed by Maynard, either individually or in collaboration with Clapp; to determine the dates on which each of these taxa became available; and to locate and to restrict the name-bearing type for each taxon to a single specimen, when necessary by the selection of a lectotype or designation of a neotype. As noted in ICZN Article 61.1 (1999: 63), "The fixation of a name-bearing type of a nominal taxon provides the objective standard of reference for the application of the name it bears." Providing objective standards for all of Maynard's taxa is a necessary first step toward pruning the "all but impenetrable taxonomic thicket" that has been a hallmark of, and an impediment to, studies of the Cerionidae.

MATERIALS AND METHODS

The publications listed in Table 1 were surveyed for descriptions of species-level taxa. The species-level taxa are listed chro-

nologically according to the date the taxa became available and in order of publication to the extent possible. For cases in which a taxon name appeared only on a plate caption but not in the text, it is listed at the end of the taxa published in the same issue or on the same date. This list was compared with similar compilations in Batchelder (1951) and in Clench's (1957) catalog of the Cerionidae. We do not include misspellings of Maynard's taxa by subsequent authors (e.g., Batchelder, 1951; Clench, 1957; Pilsbry, 1901–02) or Maynard's uses or misspellings of other authors' taxa. Maynard's not infrequent misspellings of his own taxa, likely introduced when he set the type, are reconciled, usually with the accepted spelling of the taxon (see however, *S. nivia,* taxa 26 and 72), and are also included in the alphabetical index of Maynard's taxa.

Each validly introduced taxon is numbered sequentially and is followed by one or more citations, including the valid taxon description (**in bold**), which for several taxa differs from the intended taxon description. Also included are details of specimens associated with the term "type" within the intended taxon description, published measurements, and the number of specimens examined.

The number and the status of name-bearing type specimens for each taxon are determined within the context of the most recent edition of the ICZN (1999). This determination is based on information in the original description, other portions of the same publication, subsequent publications, and works of other authors, as well as on specimens traceable to Maynard's collection now in the collections of the MCZ. Several of Maynard's taxa were not represented in his collection when it reached the Museum, as confirmed by an examination of the MCZ catalog. For these taxa, efforts were made to locate specimens traceable to Maynard in the collections of the MCZ and the National Museum of Natural History, Smithsonian Institution (USNM), Academy of Natural Sciences of Philadelphia (ANSP), the Field Museum of Natural History (FMNH), Florida Museum of Natural History (FLMNH), and Museum of Biological Diversity, The Ohio State University (OSU). When necessary, a lectotype is selected or a neotype is designated from among specimens in these museums to restrict the name-bearing type for each taxon to a single specimen. This is followed by measurements of the single name-bearing type, the type locality for the taxon, and remarks pertaining to the taxon. Images of the apertural and right lateral views are also included.

Comparisons with published measurements and figures have been made when selecting or verifying primary type specimens (Recommendation 74B, ICZN, 1999: 83). It should be noted from the onset that some variation is to be expected in measurements of length and far more in measurements of width, as these depend not only on the accuracy of the instrument used (ruler vs. digital caliper), but also on how the measurements were made (length measured parallel to the axis of coiling vs. maximum length; width of the cylindrical portion of the shell vs. maximum width including flaring aperture). Even the best of Maynard's illustrations, while generally adequate for distinguishing taxa, are rarely precise enough to differentiate among the often numerous specimens in the type series. Turner (1957: 140) quoted from Maynard's unpublished autobiography, "When I was a child I took a great liking to the art of wood engraving. Not because I had ever seen any of the work done, for I had not, but with the idea in mind that I should like the work, I consulted a neighbor who was a wood engraver. After questioning me as to my ability to make drawings and after not finding me at all proficient in that art, he said emphatically that I would not succeed as an engraver, so I abandoned that project." Turner went on to write "It is interesting to see that in later years he made all of his own illustrations and wood engravings, as

well as hand coloring many of his plates. These illustrations are remarkably well done considering his complete lack of training."

Contributions to the History of the Cerionidae, published in 12 numbers between 1919 and 1926, presents a variety of nomenclatural complexities for several of the taxa proposed within its pages. Most involve the consequences of unintended nomenclatural acts upon the authorship of the taxa, the dates on which names became available, and the determination of their primary types. Strict interpretation within the context of the International Code of Zoological Nomenclature (ICZN, 1999) clearly contradicts the authors' intentions in most of these cases.

In the preface to this work, Maynard (1919a: 1) stated that he had "written Parts One and Three and the descriptions of the animals and their habitats in Part Two, but that the descriptions of the shells in this part have been written with the collaboration of Mrs. William F. [Nellie A.] Clapp, and the names of new species should be credited to us jointly." Part One is explicitly delimited as spanning pages 3–112, but also included figures 1–89, and was published with plates 5–10, 10*, and 11–19. Part Two is labeled as beginning on page 113 and would appear, on the basis of content and style, to end on page 153. It contains one map and no figures and includes plates 1–4 and 20–37 but also refers to illustrations on plates 38–48. Plates 38–43 were published later, together with the text portions of Part Three, whereas plates 44–48 were never published. What appear, on the basis of content and style, to be continuations of Part One span pages 154–163 and 178–180. A more detailed "Description of Species" that begins on page 164 and, except for pp. 178–180, continues until the last page (p. 218), is presumed to be Part Three, although it is nowhere identified as such. It would appear that Maynard intended to publish additional text and plates.

In the introduction to Part Two, Maynard (1920d: 113) again confirmed that new species "should be credited to Maynard and Clapp." However, it is clear that Maynard retained authorship of the work in the preface (Maynard, 1919a: 1). He subsequently (Maynard, 1924c: 1) referred to this work as "my *Contributions to the History of the Cerionidae* began in 1919." Thus, the authorship of taxa proposed in Part Two should be cited as Maynard and Clapp *in* Maynard, 1920–25. Taxa inadvertently introduced in other portions of this work are attributed to Maynard, unless there was an indication to the contrary (e.g., taxon name followed by "M. & C." in the figure caption).

The first six issues of *Contributions to the History of the Cerionidae* and a portion of the seventh (Maynard, 1919a–1920d) comprise Part One and contain extensive notes on Cerionidae, including comments on the age and ecology of living and fossil Cerions, postulated laws governing the evolution of the family, and a list of characteristics deemed useful for differentiating groups or species. Unfortunately, Maynard used the names of several of the taxa intended to be described in Part Two of this work to illustrate particular morphological features. These names often appeared in figure captions or in conjunction with references to illustrations that would be published later, but still before the intended taxon descriptions. In some cases, this resulted in the creation of nomina nuda, in others, to inadvertent but nomenclaturally valid species descriptions. Although these inadvertent species descriptions rarely alter the intended concept of the taxon, they do affect the date, authorship, and type designations for these taxa.

Supplemental information for each of Maynard's *Cerion* taxa, including the text of the original description and images of the primary types in color, can be found on the *Cerion* website (http://invertebrates.si.edu/cerion).

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THE *CERION* TAXA OF CHARLES JOHNSON MAYNARD

All species-level taxa within the family Cerionidae that were validly proposed by Maynard, either individually or in collaboration with Clapp, are listed chronologically according to the date the taxa became available and in order of publication to the extent possible. In cases in which a taxon name appeared only on a plate caption but not in the text, it is listed at the end of the taxa published in the same issue or on the same date. An alphabetical listing of the taxa (as well as their misspellings) is provided in the index at the end of this work.

Each validly introduced taxon is numbered sequentially and is followed by one or more citations, including the valid taxon description (**in bold**), which for several taxa differs from the intended taxon description. Also included are details of specimens associated with the term "type" within the intended taxon description, published measurements, and the number of specimens examined. These details are provided as they appeared in the original publications and typographical errors have not been corrected. Type localities are also provided as originally published, with supplemental information included in square brackets.

Taxon 1. *Strophia pannosa* **Maynard, 1889a [April]: 10–11, pl. 1, figs. 2, 13, pl. 2, figs. 1, 1B, 1C, 1D.** Examined 400 specimens. Original description lists sizes of two "types" given as 1.27 by .57 and 1.23 by .50 [inches; 32.3 by 14.5 and 31.2 by 12.7 mm]. Caption to plate 2, figure 1 states "Strophia pannosa, front view of type shell."

Type Material. The original description provided measurements for two "type" specimens, which are thus syntypes. One of these syntypes was illustrated. The remaining 398 specimens are, according to Article 72.4.6 (ICZN, 1999: 77), expressly excluded from the type series. Therefore, there can be no paratypes, and any specimens labeled as such are mislabeled. Clench (1964: 368, pl. 63, fig. 1) designated and figured as lectotype MCZ 246343, noting, "In several cases Maynard failed to select a holotype, so lectotypes have been selected here which agree as closely as can be determined with his descriptions and measurements" (Clench, 1964: 370). This lectotype approximates the measurements of the smaller of the two syntypes. The remaining syntype became the paralectotype.

Lectotype Measurements. Length 31.0 mm, diameter (excluding lip) 13.1 mm; aperture height (including lip) 11.6 mm, aperture width (including lip and peristome) 10.1 mm.

Type Locality. West end of Little Cayman, Cayman Islands.

Remarks. Clench (1964: 368) regarded this taxon as a valid species and provided an extensive synonymy.

Taxon 2. *Strophia levigata* **Maynard, 1889a [April]: 12–13, pl. 2, figs. 2, 2B.** Examined 150 specimens. Original description lists sizes of two "types" given as 1.25 by .52 and 1.15 by .48 [inch-

es; 31.8 by 13.2 and 29.2 by 12.2 mm]. Caption to plate 2, figure 2, "Strophia levigata, front view of type shell."

Type Material. The original description provided measurements for two "type" specimens, which are thus syntypes. One of these syntypes was illustrated. The remaining 148 specimens are, according to Article 72.4.6 (ICZN, 1999: 77), expressly excluded from the type series. Therefore, there can be no paratypes, and any specimens labeled as such are mislabeled. Clench (1964: 368, pl. 63, fig. 2) designated and figured as lectotype MCZ 247021, noting, "In several cases Maynard failed to select a holotype, so lectotypes have been selected here which agree as closely as can be determined with his descriptions and measurements" (Clench, 1964: 370). This specimen is within 5% of the length of either of the syntypes but closer to the larger syntype in width. The remaining syntype became the paralectotype.

Lectotype Measurements. Length 30.9 mm, diameter (excluding lip) 14.3 mm; aperture height (including lip) 13.1 mm, aperture width (including lip and peristome) 11.4 mm.

Type Locality. West end of Little Cayman, Cayman Islands.

Remarks. Clench (1964: 368) regarded this taxon as a synonym of *Cerion pannosum* (Maynard, 1889).

Taxon 3. *Strophia intermedia* **Maynard, 1889a [April]: 13–15, pl. 2, figs. 3, 3B.** Examined 3,000 specimens. Original description lists sizes of two "types" given as .90 by .40 and .88 by .48 [inches; 22.9 by 10.2 and 22.4 by 12.2 mm]. Caption to plate 2, figure 3, "Strophia intermedia, front view of type shell."

Type Material. The original description provided measurements for two "type" specimens, which are thus syntypes. One of these syntypes was illustrated. The remaining 2,998 specimens are, according to Article 72.4.6 (ICZN, 1999: 77), expressly excluded from the type series. Therefore, there can be no paratypes, and any specimens labeled as such are mislabeled. Clench (1964: 368, pl. 63, fig. 3) listed and figured as Holotype MCZ 76067. This specimen, which is closer to the larger syntype in length and to the smaller syntype in width, cannot be the holotype, as two syntypes had been listed. Clench's listing cannot be accepted as a lectotype designation. Article 74.5 (ICZN, 1999: 83) states, "When the original work reveals that the taxon had been based on more than one specimen, a subsequent use of the term 'holotype' does not constitute a valid lectotype designation unless the author, when wrongly using that term, explicitly indicated that he or she was selecting from the type series that particular specimen to serve as the name-bearing type." This specimen (MCZ 76067) is here selected as the lectotype. The remaining syntype becomes the paralectotype.

Lectotype Measurements. Length 24.8 mm, diameter (excluding lip) 12.0 mm; aperture height (including lip) 10.1 mm, aperture width (including lip and peristome) 8.8 mm.

Type Locality. Coast along the south side of Little Cayman, Cayman Islands.

Remarks. Clench (1964: 368) regarded this taxon as a synonym of *Cerion pannosum* (Maynard, 1889).

Taxon 4. *Strophia acuta* **Maynard, 1889a [April]: 15–17, pl. 2, figs. 4, 4B.** Examined 500 specimens. Sizes of two "types" given as .94 by .40 and .94 by .38 [inches; 23.9 by 10.2 and 23.9 by 9.7

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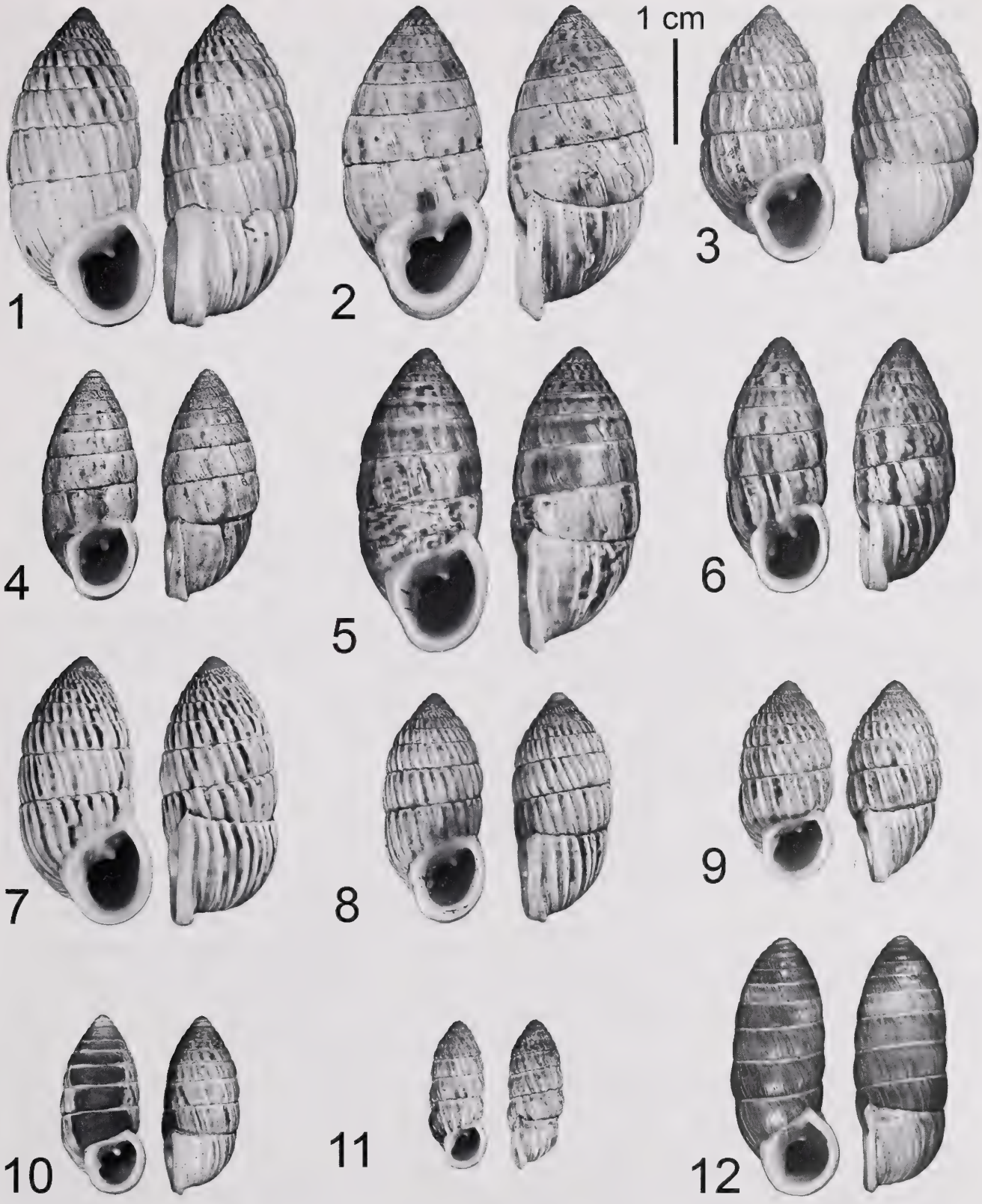
Figures 1–12. Taxon 1. *Strophia pannosa* Maynard, 1889. Lectotype MCZ 246343. West end of Little Cayman, Cayman Islands. Taxon 2. *Strophia levigata* Maynard, 1889. Lectotype MCZ 247021. West end of Little Cayman, Cayman Islands. Taxon 3. *Strophia intermedia* Maynard, 1889. Lectotype MCZ 76067. South side of Little Cayman, Cayman Islands. Taxon 4. *Strophia acuta* Maynard, 1889. Lectotype MCZ 247022. Field inland from the south coast of Little Cayman, Cayman Islands. Taxon 5.



Strophia festiva Maynard, 1889. Lectotype MCZ 247023. Fields along path, near center of Little Cayman, Cayman Islands. Taxon 6. *Strophia picta* Maynard, 1889. Lectotype MCZ 247019. West end of Little Cayman, Cayman Islands. Taxon 7. *Strophia lineota* Maynard, 1889. Lectotype MCZ 246346. South side of Little Cayman, Cayman Islands. Taxon 8. *Strophia copia* Maynard, 1889. Lectotype MCZ 76065. West end of Cayman Brac, Cayman Islands. Taxon 9. *Strophia parva* Maynard, 1889. Lectotype MCZ 246423. West end of Cayman Brac, Cayman Islands. Taxon 10. *Strophia glaber* Maynard, 1889. Lectotype MCZ 246344. West end of Cayman Brac, Cayman Islands. Taxon 11. *Strophia nana* Maynard, 1889. Lectotype MCZ 246737. West end of Little Cayman, Cayman Islands, near intersection of two paths. Taxon 12. *Strophia nuda* Maynard, 1889. Lectotype MCZ 356977. Near Clarence Harbor, Long Island, Bahamas.

mm]. Caption to plate 2, figure 4, "Strophia acuta, front view of type shell."

Type Material. The original description provided measurements for two "type" specimens, which are thus syntypes. One of these syntypes was illustrated. The remaining 498 specimens are, according to Article 72.4.6 (ICZN, 1999: 77), expressly excluded from the type series. Therefore, there can be no paratypes, and any specimens labeled as such are mislabeled. Clench (1964: 368, pl. 63, fig. 4) designated and figured as lectotype MCZ 247022, noting, "In several cases Maynard failed to select a holotype, so lectotypes have been selected here which agree as closely as can be determined with his descriptions and measurements" (Clench, 1964: 370). This specimen approximates the narrower of the two syntypes in width. The remaining syntype became the paralectotype.

Lectotype Measurements. Length 22.2 mm, diameter (excluding lip) 9.2 mm; aperture height (including lip) 8.6 mm, aperture width (including lip and peristome) 7.2 mm.

Type Locality. Field inland from the south coast of Little Cayman, Cayman Islands.

Remarks. Clench (1964: 368) regarded this taxon as a synonym of *Cerion pannosum* (Maynard, 1889).

Taxon 5. *Strophia festiva* **Maynard, 1889a [April]: 17–18, pl. 2, figs. 5, 5B, C.** Examined 22 specimens. Sizes of two "types" given as 1.20 by .50 and 1.18 by .48 [inches; 30.5 by 12.7 and 30.0 by 12.2 mm]. Caption to plate 2, figure 5, "Strophia festiva, front view of type shell."

Type Material. The original description provided measurements for two "type" specimens, which are thus syntypes. One of these syntypes was illustrated. The remaining 20 specimens are, according to Article 72.4.6 (ICZN, 1999: 77), expressly excluded from the type series. Therefore, there can be no paratypes, and any specimens labeled as such are mislabeled. Clench (1964: 368, pl. 63, fig. 5) designated and figured as lectotype MCZ 247023, noting, "In several cases Maynard failed to select a holotype, so lectotypes have been selected here which agree as closely as can be determined with his descriptions and measurements" (Clench, 1964: 370). This specimen approximates the smaller of the two syntypes in length. The remaining syntype became the paralectotype.

Lectotype Measurements. Length 29.7 mm, diameter (excluding lip) 12.3 mm; aperture height (including lip) 12.1 mm, aperture width (including lip and peristome) 10.2 mm.

Type Locality. Fields along path, near center of Little Cayman, Cayman Islands.

Remarks. Clench (1964: 368) regarded this taxon as a synonym of *Cerion pannosum* (Maynard, 1889).

Taxon 6. *Strophia picta* **Maynard, 1889a [April]: 18–20, pl. 2, figs. 6, 6B.** Examined 75 specimens. Sizes of two "types" given as .96 by .40 and .86 by .39 [inches; 24.4 by 10.2 and 21.8 by 9.9 mm]. Caption to plate 2, figure 6, "Strophia picta, front view of type shell."

Type Material. The original description provided measurements for two "type" specimens, which are thus syntypes. One of these syntypes was illustrated. The remaining 73 specimens are, according to Article 72.4.6 (ICZN, 1999: 77), expressly excluded from the type series. Therefore, there can be no paratypes, and any specimens labeled as such are mislabeled. Clench (1964: 368, pl. 63, fig. 6) designated and figured as lectotype MCZ 247019, noting, "In several cases Maynard failed to select a holotype, so lectotypes have been selected here which agree as closely as can be determined with his descriptions and measurements" (Clench, 1964: 370). This specimen approximates the larger of the two syntypes in length. The remaining syntype became the paralectotype.

Lectotype Measurements. Length 24.4

mm, diameter (excluding lip) 9.9 mm; aperture height (including lip) 9.3 mm, aperture width (including lip and peristome) 7.8 mm.

Type Locality. West end of Little Cayman, Cayman Islands.

Remarks. Clench (1964: 368) regarded this taxon as a synonym of *Cerion pannosum* (Maynard, 1889).

Taxon 7. *Strophia lineota* **Maynard, 1889a [April]: 20–22, pl. 2, figs. 7, 7B.** Examined 1,000 specimens. Sizes of two "types" given as 1.04 by .40 and .98 by .42 [inches; 26.4 by 10.2 and 24.9 by 10.7 mm]. Caption to plate 2, figure 7, "Strophia lineota, front view of type shell."

Type Material. The original description provided measurements for two "type" specimens, which are thus syntypes. One of these syntypes was illustrated. The remaining 998 specimens are, according to Article 72.4.6 (ICZN, 1999: 77), expressly excluded from the type series. Therefore, there can be no paratypes, and any specimens labeled as such are mislabeled. Clench (1964: 368, pl. 63, fig. 7) designated and figured as lectotype MCZ 246346, noting, "In several cases Maynard failed to select a holotype, so lectotypes have been selected here which agree as closely as can be determined with his descriptions and measurements" (Clench, 1964: 370). This specimen approximates the larger of the two syntypes in length. The remaining syntype became the paralectotype.

Lectotype Measurements. Length 26.1 mm, diameter (excluding lip) 11.3 mm; aperture height (including lip) 11.0 mm, aperture width (including lip and peristome) 9.0 mm.

Type Locality. Coconut grove, south side of Little Cayman, Cayman Islands. Maynard (1889a: 21) noted that this taxon was also found near the boat landing on Cayman Brac, but was probably introduced there from Little Cayman. Clench (1957: 151, 1964: 368) listed both localities. The label accompanying the lectotype gives the locality as "S.E. side of Little Cayman Id., Cayman Ids."

Remarks. Clench (1964: 368) regarded this taxon as a synonym of *Cerion pannosum* (Maynard, 1889).

Taxon 8. *Strophia copia* **Maynard, 1889a [April]: 22–24, pl. 1, figs. 1, 3, 7–12, pl. 2, figs. 8, 8B.** Examined 10,000 specimens. Sizes of two "types" given as .90 by .40 and .95 by .40 [inches; 22.9 by 10.2 and 24.1 by 10.2 mm]. Caption to plate 2, figure 8, "Strophia copia, front view of type shell."

Type Material. The original description provided measurements for two "type" specimens, which are thus syntypes. One of these syntypes was illustrated. The remaining 9,998 specimens are, according to Article 72.4.6 (ICZN, 1999: 77), expressly excluded from the type series. Therefore, there can be no paratypes, and any specimens labeled as such are mislabeled. Clench (1964: 368, pl. 63, fig. 8) designated and figured as lectotype MCZ 76065, noting, "In several cases Maynard failed to select a holotype, so lectotypes have been selected here which agree as closely as can be determined with his descriptions and measurements" (Clench, 1964: 370). This specimen approximates the smaller of the two syntypes in length. The remaining syntype became the paralectotype.

Lectotype Measurements. Length 22.2 mm, diameter (excluding lip) 9.6 mm; aperture height (including lip) 9.0 mm, aperture width (including lip and peristome) 7.6 mm.

Type Locality. West end of Cayman Brac, Cayman Islands.

Remarks. Clench (1964: 368) regarded this taxon as a synonym of *Cerion pannosum* (Maynard, 1889). Hummelinck (1980: 59) recognized it as a distinct species.

Taxon 9. *Strophia parva* **Maynard, 1889a [April]: 24–25, pl. 2, figs. 9, 9B.** Examined about 1,000 specimens. Sizes of two "types" given as .60 by .30 and .63

by .32 [inches; 15.2 by 7.6 and 16.0 by 8.1 mm]. Caption to plate 2, figure 9, "Strophia parva, front view of type shell."

Type Material. The original description provided measurements for two "type" specimens, which are thus syntypes. One of these syntypes was illustrated. The remaining 998 specimens are, according to Article 72.4.6 (ICZN, 1999: 77), expressly excluded from the type series. Therefore, there can be no paratypes, and any specimens labeled as such are mislabeled. Clench (1964: 368, pl. 63, fig. 9) designated and figured as lectotype MCZ 246423, noting, "In several cases Maynard failed to select a holotype, so lectotypes have been selected here which agree as closely as can be determined with his descriptions and measurements" (Clench, 1964: 370). This specimen approximates the larger of the two syntypes in length. The remaining syntype became the paralectotype.

Lectotype Measurements. Length 19.1 mm, diameter (excluding lip) 9.0 mm; aperture height (including lip) 7.8 mm, aperture width (including lip and peristome) 6.6 mm.

Type Locality. West end of Cayman Brac, Cayman Islands.

Remarks. Clench (1964: 368) regarded this taxon as a synonym of *Cerion pannosum* (Maynard, 1889).

Taxon 10. *Strophia glaber* **Maynard, 1889a [April]: 25–26, pl. 2, figs. 10, 10B.** Examined 16 specimens. Sizes of two "types" given as .62 by .33 and .65 by .30 [inches; 15.7 by 8.4 and 16.5 by 7.6 mm]. Caption to plate 2, figure 10, "Strophia glaber, front view of type shell."

Type Material. The original description provided measurements for two "type" specimens, which are thus syntypes. One of these syntypes was illustrated. The remaining 14 specimens are, according to Article 72.4.6 (ICZN, 1999: 77), expressly excluded from the type series. Therefore, there can be no paratypes, and any specimens labeled as such are mislabeled. Clench (1964: 368, pl. 63, fig. 10) designated and figured as lectotype MCZ 246344, noting, "In several cases Maynard failed to select a holotype, so lectotypes have been selected here which agree as closely as can be determined with his descriptions and measurements" (Clench, 1964: 370). This specimen approximates the larger of the two syntypes in length. The remaining syntype, MCZ 39715, became the paralectotype.

Lectotype Measurements. Length 17.6 mm, diameter (excluding lip) 7.7 mm; aperture height (including lip) 6.3 mm, aperture width (including lip and peristome) 5.9 mm.

Type Locality. West end of Cayman Brac, Cayman Islands.

Remarks. Clench (1964: 368) regarded this taxon as a synonym of *Cerion pannosum* (Maynard, 1889).

Taxon 11. *Strophia nana* **Maynard, 1889a [April]: 27–29, pl. 2, figs. 11A, B, C, D.** Examined 2,000 specimens. Sizes of two "types" given as .62 by .25 and .60 by .18 [inches; 15.7 by 6.4 and 15.2 by 4.6 mm]. Caption to plate 2, figure 11, "Strophia nana, A, front view of type shell."

Type Material. The original description provided measurements for two "type" specimens, which are thus syntypes. One of these syntypes was illustrated. The remaining 1,998 specimens are, according to Article 72.4.6 (ICZN, 1999: 77), expressly excluded from the type series. Therefore, there can be no paratypes, and any specimens labeled as such are mislabeled (e.g., Hummelinck, 1980, pl. 11, figs. g–k). Clench (1964: 373, pl. 63, fig. 14) designated and figured as lectotype MCZ 246737, noting, "In several cases Maynard failed to select a holotype, so lectotypes have been selected here which agree as closely as can be determined with his descriptions and measurements" (Clench,

1964: 370). This specimen approximates the smaller of the two syntypes in length. The remaining syntype became the paralectotype.

Lectotype Measurements. Length 14.4 mm, diameter (excluding lip) 5.4 mm; aperture height (including lip) 5.2 mm, aperture width (including lip and peristome) 4.1 mm.

Type Locality. West end of Little Cayman, Cayman Islands, near intersection of two paths. Maynard (1889a: 28) noted "the Dwarf Strophias [*Strophia nana*] occur in a space which is only five or six yards wide by twenty long . . . I consider that this species has the most restricted range of any animal with which I am acquainted."

Remarks. Clench (1964: 373) regarded this taxon to be a valid species.

Taxon 12. *Strophia nuda* **Maynard, 1889a [April]: 29, pl. 2, figs. 12, 12B.** Examined three specimens. Sizes of two "types" given as 1.00 by .39 and .82 by .32 [inches; 25.4 by 9.9 and 20.8 by 8.1 mm]; other specimen .89 by .38 [inches; 22.6 by 9.6 mm]. Caption to plate 2, figure 12, "Strophia nuda, front view of type shell."

Type Material. The original description provided measurements for two "type" specimens, which are thus syntypes. One of these syntypes was illustrated. Of the three lots at the MCZ that were possible types [MCZ 39713, MCZ 76267, MCZ, 87985], one, MCZ 76267, contained six specimens, the other two lots have one specimen each. Maynard (1889a: 29) wrote, ". . . I have only three of this singular *Strophia* . . ." Nevertheless, MCZ 76267 contains Maynard's label with the term "type," and a later MCZ label that is annotated on the back, "Only three specimens in original series given by Maynard—He has apparently added to them!!!"

The length and width of each of the specimens in each of these three lots were measured. None of the specimens in any of the lots matched Maynard's published measurements exactly, although the largest specimen [24.9 by 9.7 mm] came closest to the measurements of the larger of the two syntypes listed by Maynard. When the ratios of length to width were computed and compared with ratios of published type measurements, this same specimen matched to within 1%.

None of the remaining specimens came as close to matching either the linear measurements or the length to width ratio of the other type, although the single specimen in MCZ 39713 came within 5%. A specimen in MCZ 76267 sectioned to expose the columellar axis comes closest to the measurements given for the "other specimen." The largest specimen (24.9 mm) from MCZ 76267 was therefore selected as the lectotype and recatalogued as MCZ 356977. The specimen in MCZ 39713 becomes the paralectotype. The remaining specimen is, according to Article 72.4.6 (ICZN, 1999: 77), expressly excluded from the type series. Therefore, there can be no paratypes and any specimens labeled as such are mislabeled.

Lectotype Measurements. Length 24.9 mm, diameter (excluding lip) 9.7 mm; aperture height (including lip) 8.7 mm, aperture width (including lip and peristome) 7.3 mm.

Type Locality. Near Clarence Harbor, Long Island, Bahamas.

Taxon 13. *Strophia ianthina* **Maynard, 1889a [April], pl. 2, figs. 13, 13B.** Caption to plate 2, figure 13, "Strophia ianthina, front view of type shell"; Maynard, 1889b [July]: 69–70. Text noted 300 specimens examined. Sizes of two "types" given as 1.15 by .37 and 1.00 by .36 [inches; 29.2 by 9.4 and 25.4 by 9.1 mm].

Nomenclatural Remarks. The illustrations (Maynard, 1889a, pl. 2, figs. 13, 13B) and caption were published prior to the text. The taxon thus dates from the publication of the name in the caption accompanying the illustrations, not from the sub-

sequently published text (Article 12.2.7, ICZN, 1999: 17).

Type Material. The specimen represented in the figure was identified as the "type shell" and is therefore the holotype (Article 73.1.4, ICZN, 1999: 80). Although there was no mention of other specimens in the plate caption, the remaining 299 specimens enumerated in the text portion published 3 months later were likely available to Maynard at the time the plate was prepared and are thus part of the type series [Article 72.4.1.1, ICZN, 1999: 76], serving as paratypes of *Strophia ianthina.* There was no specimen labeled "Holotype" at the MCZ. Lot number MCZ 39714 contains one specimen labeled "paratype," and MCZ 10317 contained two adult specimens, also labeled "paratypes." The larger of these two specimens closely approximates the figured specimen in size and proportions. This is here considered to be the figured specimen and therefore the holotype.

Holotype Measurements. Length 27.6 mm, diameter (excluding lip) 10.1 mm; aperture height (including lip) 9.8 mm, aperture width (including lip and peristome) 8.1 mm.

Type Locality. Between southern shore of Inagua [Bahamas] and the extensive salt lake about 25 miles from Mathewstown.

Remarks. Application of Article 12.2.7 (ICZN, 1999: 17) does not alter the authorship of this taxon, but accelerates its publication by 3 months. Clench (1959: 45) listed this taxon as a synonym of *Cerion (Diacerion) rubicundum* (Menke, 1829).

Taxon 14. *Strophia palida* **Maynard, 1889a [April], pl. 2 figs. 14, 14B.** Caption to plate 2, figure 14, "Strophia palida, front view of type shell." *Strophia pallida* Maynard, 1889b [July]: 70–71. Text noted 25 specimens examined and mentioned the sizes of two "types" given as 1.03 by .36 and 1.03 by .33 [inches; 26.2 by 9.1 and 26.2 by 8.4 mm].

Nomenclatural Remarks. The illustrations [pl. 2, figs. 14, 14B] and caption were published prior to the text. The taxon thus dates from the publication of the name in the caption accompanying the illustrations, not from the subsequently published text (Article 12.2.7, ICZN, 1999: 17).

Type Material. The specimen represented in the figure is identified as the "type shell" and is therefore the holotype (Article 73.1.4, ICZN, 1999: 80). Although there was no mention of other specimens in the plate caption, the remaining 24 specimens enumerated in the text portion published 3 months later were likely available to Maynard at the time the plate was prepared and are thus part of the type series [Article 72.4.1.1, ICZN, 1999: 76], serving as paratypes of *Strophia palida.* Lot number MCZ 76250 contained two specimens, one adult and the other juvenile, as well as multiple labels that state "type," "Holotype," and "paratype." The adult specimen is a close approximation to the illustration and is here considered to be the figured specimen and therefore the holotype. The juvenile specimen is a paratype.

Holotype Measurements. Length 26.1 mm, diameter (excluding lip) 8.8 mm; aperture height (including lip) 8.7 mm, aperture width (including lip and peristome) 6.9 mm.

Type Locality. In cultivated fields on slopes of hills bordering the southern

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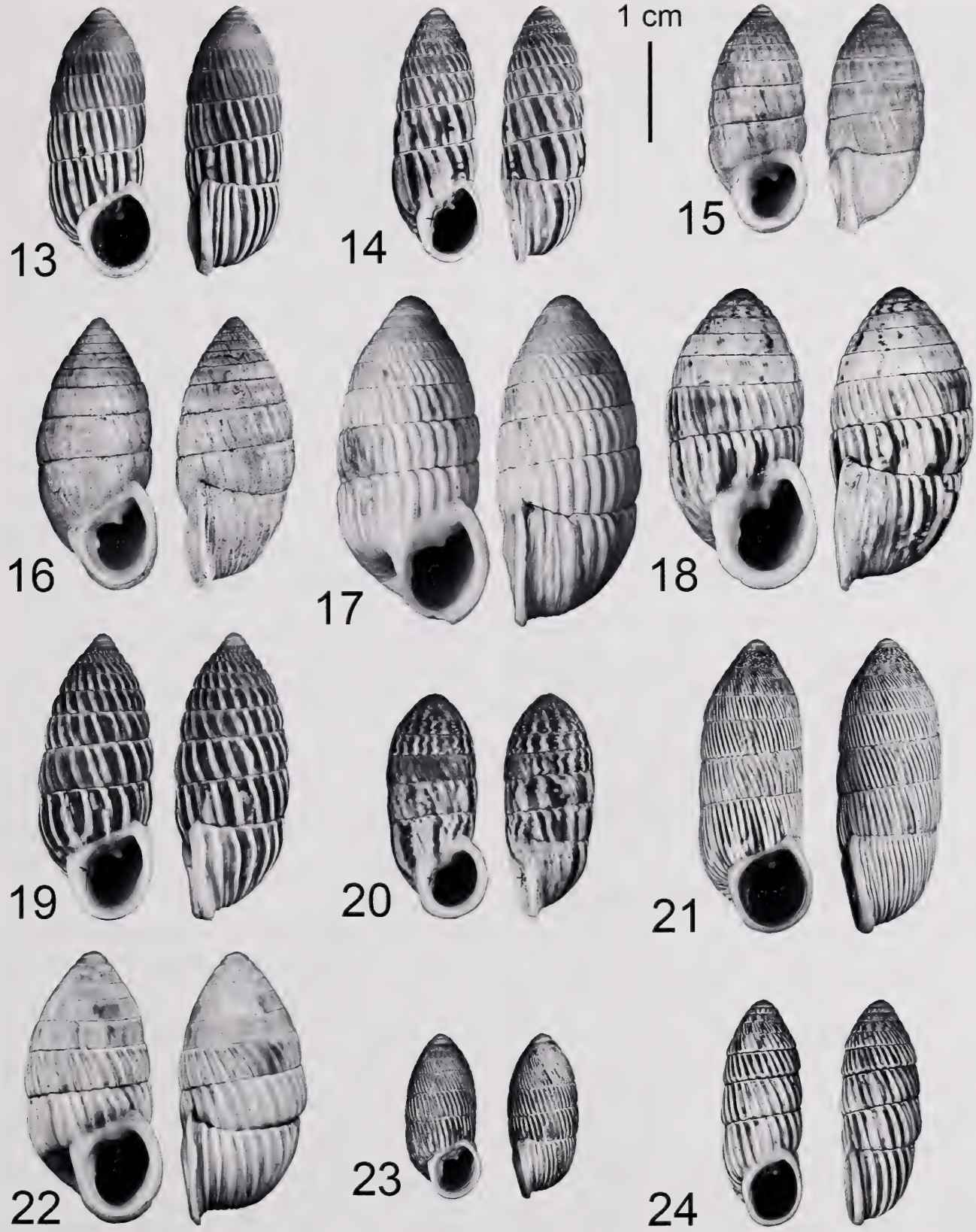
Figures 13–24. Taxon 13. *Strophia ianthina* Maynard, 1889. Holotype MCZ 10317. Between southern shore of Inagua [Bahamas] and the extensive salt lake about 25 miles from Mathewstown. Taxon 14. *Strophia palida* Maynard, 1889. Holotype MCZ 76250. Hills bordering the southern shore of Inagua, Bahamas, 15–20 miles from Mathewstown. Taxon 15. *Strophia perplexa* Maynard, 1889. Holotype MCZ 246345. About 2 miles from the western end of Cayman Brac, Cayman Islands. Taxon 16. *Strophia nitela* Maynard, 1889. Holotype MCZ 247020. Path, west end of Little Cayman, Cayman Islands. Taxon 17. *Strophia*



alba Maynard, 1889. Holotype MCZ 76150. West coast of Rum Cay, Bahamas, near salt pond. Taxon 18. *Strophia lentiginosa* Maynard, 1889. Holotype MCZ 83132. Interior of Rum Cay, Bahamas. Taxon 19. *Strophia fusca* Maynard, 1889. Holotype MCZ 76069. West end of Little Cayman, Cayman Islands. Taxon 20. *Strophia inflata* Maynard, 1889. Holotype MCZ 76400. Salina Point, Auklin Islands, Bahamas. Taxon 21. *Strophia dallii* Maynard, 1889. Holotype MCZ 76294. Inagua. Taxon 22. *Strophia brownei* Maynard, 1889. Neotype USNM 58085. Rum Key, Bahamas, near the north side. Taxon 23. *Strophia viola* Maynard, 1889. Holotype MCZ 76407. Type locality not published, but Inagua, Bahamas, on the original label. Taxon 24. *Strophia orbicularia* Maynard, 1889. Holotype MCZ 76408. Inagua, Bahamas.

shore of Inagua [Bahamas], 15–20 miles from Mathewstown.

Remarks. Application of Article 12.2.7 (ICZN, 1999: 17) does not alter the authorship of this taxon but accelerates its publication by 3 months. The publication of the plate and its caption, on which the taxon name is spelled *palida* (one "l") preceded the publication of the text, in which the taxon name is spelled *pallida* (two "l"s).

Although it seems clear that Maynard intended the taxon to be known as *pallida,* it is not possible to consider *palida* as an "incorrect original spelling" within the confines of Article 32.5.1 (ICZN, 1999: 39) because there is no clear evidence to suggest an alternative spelling within the original publication itself. This taxon was listed as *S. pallida* by Clench (1957: 156). Clench (1959: 45) included this taxon [as *pallida*] in the synonymy of *Cerion* (*Diacerion*) *rubicundum* (Menke, 1829).

Taxon 15. *Strophia perplexa* **Maynard, 1889b [July]: 71–72, pl. 7, figs. 15, 1Aa, text figs. 7A, B** [plate and text figures identical]. Examined 300 specimens. Size of type given as .90 by .40 [inches; 22.9 by 10.2 mm]. Caption to plate 7, figure 15, "Strophia perplexa, front view of type shell."

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. The remaining 299 specimens are paratypes. Clench (1964: 368, pl. 63, fig. 11) designated and figured as lectotype MCZ 246345. This specimen is here considered to be the originally designated holotype.

Holotype Measurements. Length 23.7 mm, diameter (excluding lip) 10.2 mm; aperture height (including lip) 9.2 mm, aperture width (including lip and peristome) 7.9 mm.

Type Locality. Cayman Brac, [Cayman Islands] barren rocky section about 2 miles from the western end of the key ¼ mile from the south shore.

Remarks. Clench (1964: 368) regarded this taxon as a synonym of *Cerion pannosum* (Maynard, 1889).

Taxon 16. *Strophia nitela* Maynard**, 1889b [July]: 73–74, pl. 7, figs. 16, 16A, text figs. 8A, B** [plate colored and text figures uncolored, otherwise identical]. Examined 300 specimens. Size of type given as 1.10 by .50 [inches; 27.9 by 12.7 mm]. Caption to plate 7, figure 16, "Strophia nitela, front view of type shell; 16A, left side of same individual."

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. The remaining 299 specimens are paratypes. Clench (1964: 368, pl. 63, fig. 12) designated and figured as lectotype MCZ 247020. This specimen is here considered to be the originally designated holotype.

Holotype Measurements. Length 27.5 mm, diameter (excluding lip) 11.8 mm; aperture height (including lip) 11.1 mm, aperture width (including lip and peristome) 9.2 mm.

Type Locality. Margins of path, west end of Little Cayman, Cayman Islands.

Remarks. Clench (1964: 368) regarded this taxon as a synonym of *Cerion pannosum* (Maynard, 1889).

Taxon 17. *Strophia alba* **Maynard, 1889b [July]: 74–75, pl. 7, figs. 17, 17A, B, text figs. 9A, B, text fig. 11 (sic) (11 in caption, 10 on figure)** [plate and text figures identical]. Examined 250 specimens. Size of "type" given as 1.42 by .55 [inches; 36.1 by 14.0 mm]. Caption to plate 7, figure 17, "Strophia alba, front view of type shell; 17a, left side of same individual."

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. The remaining 249 specimens are paratypes. There was no specimen labeled "Holotype" at the MCZ. Lot MCZ 76150

was labeled "Paratypes" and contained four specimens: two intact adults, a sectioned adult, and a juvenile. The largest intact shell is 33.0 by 14.0 mm. Although this is shorter than the published length of the type, it does match closely the size and proportions of the figured specimen, which the caption identifies as the type. This specimen (MCZ 76150) is here considered to be the originally designated holotype. Paratypes include MCZ 356978 (three remaining specimens from MCZ 76150), MCZ 39718 (one specimen), MCZ 10243 (two specimens), and USNM 420067 (nine specimens).

Holotype Measurements. Length 33.0 mm, diameter (excluding lip) 14.0 mm; aperture height (including lip) 12.6 mm, aperture width (including lip and peristome) 10.2 mm.

Type Locality. West coast of Rum Cay [Bahamas], near salt pond.

Remarks. Clench (1934: 208) listed this taxon as a junior synonym of *Cerion lentiginosum* (Maynard, 1889).

Taxon 18. *Strophia lentiginosa* **Maynard, 1889b [July]: 75–76, pl. 7, figs. 18, 18a, text figs. 11a, b** [plate colored, text figures uncolored, otherwise identical]. Examined 150 specimens. Size of types [sic] given as 1.23 by .54 [inches; 31.2 by 17.7 mm]. Caption to pl. 7, fig. 18, "Strophia lentiginosa, front view of type shell; 18a, left side of the same individual."

Type Material. The original description provided a single set of measurements, but states "types" rather than type. This is presumed to be a typographical error, with the measurements applying to a single specimen, the holotype, which was illustrated. The remaining 149 specimens are paratypes. Clench (1934: 209, pl. 2, fig. D) listed and illustrated MCZ 83132 as the holotype. This specimen is the originally designated holotype. Paratypes include: MCZ 10294, one paratype; MCZ 86701, one paratype; MCZ 76073, 13 paratypes.

Holotype Measurements. Length 30.9 mm, diameter (excluding lip) 14.2 mm; aperture height (including lip) 13.4 mm, aperture width (including lip and peristome) 10.4 mm.

Type Locality. Interior of Rum Cay [Bahamas].

Remarks. Clench (1934: 208) regarded *S. lentiginosa* to be the senior synonym of *S. alba* Maynard, 1889 (Taxon 17), and of *S. brownei* Maynard, 1890 (Taxon 22).

Taxon 19. *Strophia fusca* **Maynard, 1889b [July]: 77–78, pl. 7, figs. 19, 19a, text figs. 12A, B** [plate colored and text figures uncolored, otherwise identical]. Examined 46 specimens. Size of type given as 1.25 by .45 [inches; 31.8 by 11.4 mm]. Caption to plate 7, figure 19, "Strophia fusca, front view of type shell; 18a, left side of same individual."

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. The remaining 45 specimens are paratypes. Clench (1964: 368, pl. 63, fig. 13) listed and illustrated MCZ 76069 as the holotype. This specimen is the originally designated holotype.

Holotype Measurements. Length 28.48 mm, diameter (excluding lip) 11.51 mm; aperture height (including lip) 10.41 mm, aperture width (including lip and peristome) 8.97 mm.

Type Locality. West end of Little Cayman, Cayman Islands.

Remarks. Clench (1964: 368) regarded this taxon to be a synonym of *Cerion pannosum* (Maynard, 1889).

Taxon 20. *Strophia inflata* **Maynard, 1889b [July], pl. 7, figs. 21, 21a.** Caption to plate 7, figure 21 "Strophia inflata, front view of type shell; 21a, left side of same individual"; Maynard, 1889c [October]: 126–127, text fig. 30A, B [plate colored and text figures uncolored, otherwise identical]. Text noted 25 specimens examined. Size of "types"

[sic] given as .90 by .35 [inches; 22.9 by 8.9 mm].

Type Material. The specimen represented in the figure is identified as the "type shell" and is therefore the holotype (Article 73.1.4, ICZN, 1999: 80). Although there was no mention of other specimens in the plate caption, the remaining 24 specimens enumerated in the text portion published 3 months later were likely available to Maynard at the time the plate was prepared and are thus part of the type series [Article 72.4.1.1, ICZN, 1999: 76], serving as paratypes of *Strophia inflata.* Lot MCZ 76400, labeled "Holotype," containing a single specimen that closely approximates the original figure, and accompanied by a note in Maynard's handwriting, is here recognized as the holotype.

Holotype Measurements. Length 22.9 mm, diameter (excluding lip) 9.2 mm; aperture height (including lip) 8.5 mm, aperture width (including lip and peristome) 7.5 mm.

Type Locality. Salina Point, Auklin [Acklins] Islands, Bahamas.

Remarks. Application of Article 12.2.7 (ICZN, 1999: 17) does not alter the authorship of this taxon but accelerates its publication by 3 months. Maynard (1889c: 127) noted that the specimens on which he based this taxon were from the collection of the Boston Society of Natural History. Maynard (1919b, pl. 8, figs. 5, 6) reillustrated the holotype. Clench (1963: 408) included this taxon in the synonymy of *Cerion* (*Multistrophia*) *marmoratum* (Pfeiffer, 1847).

Taxon 21. *Strophia dallii* **Maynard, 1889c [October]: 128–135, pl. 13, figs. 23, 23a [plate labeled as pl. 16, but there are no plates 13–15, two figs. each 1B* on plate], text figs. 32, A, o, e, fig. 33** [plate colored, text figures uncolored, otherwise identical except that text figure has b and d labeled]. Examined 25 specimens. Size of type given as 1.20 by .42 [inches; 30.5 by 10.7 mm]. Caption to plate 16, figure 1b*, "Strophia dalli, right hand figure, front view of type; left, right view of same."

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. The remaining 24 specimens are paratypes. No specimen labeled as the holotype was found at the MCZ. Lot MCZ 76294 was labeled "Paratype" and contained three adult specimens together with a note in Maynard's hand containing the term "type." Of the three specimens only one closely approximates both the measurements (including proportions) and the figures. This specimen is here considered to be the originally designated holotype. The remaining two specimens (now MCZ 356979) and a single specimen (MCZ 39707) are paratypes.

Holotype Measurements. Length 30.0 mm, diameter (excluding lip) 10.7 mm; aperture height (including lip) 10.4 mm, aperture width (including lip and peristome) 8.6 mm.

Type Locality. Maynard (1889c: 135) wrote, "The first specimen of Dall's Strophia that I ever saw, I found in my Bahamian collection of shells, but unfortunately labeled so that it was uncertain whether it came from Inagua or not. Later I found a few of this species in the collection of Mr. James A. Southwick, but again I was unfortunate in not getting the locality. It was only upon receiving a series of the Smithsonian Strophias, kindly forwarded to me by Dr. Dall, that I found this species labeled as coming from Inagua."

Remarks. Clench (1934: 217) reported on specimens from Sheep Cay, western Great Inagua, but commented that these differed from Maynard's types. Clench (1959: 46) recognized this taxon as *Cerion* (*Diacerion*) *dalli* (Maynard, 1889).

Taxon 22. *Strophia brownei* **Maynard, 1889c [October], pl. 16, figs. 4A, B.** Caption to plate 16, figure 4A, "Strophia

brownei, front view of type shell; 4B, right side of same"; Maynard, 1890 [January]: 196–197, text fig. 53c, d [text figures uncolored, otherwise identical to figures on pl. 16]. Text noted 25 specimens examined. Size of type given as 1.10 by .50 [inches; 27.9 by 12.7 mm].

Type Material. The illustrations and caption were published prior to the text. The taxon thus dates from the publication of the name in the caption accompanying the illustrations, not from the subsequently published text (Article 12.2.7, ICZN, 1999: 17). The specimen represented in the figure is identified as the "type shell" and is therefore the holotype (Article 73.1.4, ICZN, 1999: 80). Although there was no mention of other specimens in the plate caption, the remaining 24 specimens enumerated in the text portion published 3 months later were likely available to Maynard at the time the plate was prepared and are thus part of the type series [Article 72.4.1.1, ICZN, 1999: 76] serving as paratypes of *Strophia brownei.* Maynard noted (1890: 197) that the specimens were from the collection of Mr. Frank C. Browne and commented that he [Maynard] saw a number of specimens as he rode along the road and "fully intended to collect them as I returned, but when I passed the place in the evening, darkness prevented me from securing any, and I did not have the opportunity of visiting the locality again." This species was not listed for sale in Maynard's catalog.

The MCZ Mollusk catalog shows that two "paratypes" of *Strophia brownei* were present in Maynard's collection at the time of his death and that these specimens had been catalogued as MCZ 76288. These specimens could not be located in the MCZ collection, despite repeated searches. It is possible that most of the specimens on which Maynard based his description were returned to Browne. In an unsigned obituary of Francis C. Browne, Pilsbry (1901: 132) commented that Browne had frequently sent him specimens for identification or verification. A survey of the collections at the Academy of Natural Sciences in Philadelphia revealed that they did not contain any specimens of *Cerion brownei* nor any specimens from Rum Cay that came from Browne.

Two specimens in the USNM collections (USNM 58085) are annotated "*S. brownei* Maynard *fide* Maynard." These specimens were collected by Rawson on Rum Key and catalogued [as *Pupa mumia* Brug.] on February 4, 1886, well before *S. brownei* was published. However, a subsequent annotation on the label indicated that Maynard had identified one of these specimens as *Strophia brownei.* This specimen (USNM 58085) is here designated as the neotype of *Strophia brownei* to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of it. The remaining specimen (now USNM 1093788) is not *S. brownei* and is not a type.

Neotype Measurements. Length 27.8 mm, diameter (excluding lip) 12.8 mm; aperture height (including lip) 11.5 mm, aperture width (including lip and peristome) 8.9 mm.

Type Locality. Rum Key [Bahamas] near the north side.

Remarks. Application of Article 12.2.7 (ICZN, 1999: 17) does not alter the authorship of this taxon but accelerates its publication by 3 months (from 1890 to 1889). Clench (1934: 208) listed this taxon as a synonym of *Cerion lentiginosum* (Maynard, 1889).

Taxon 23. *Strophia viola* **Maynard, 1889c [October], pl. 16, figs. 5A, B** [no description or mention in text]. Caption to plate 16, figure 5A, "Strophia viola, front view of type; 5B, right side of same."

Type Material. The caption to the figures identified a single type specimen, the holotype. Because no other specimens were mentioned, there are no paratypes. Clench (1959, pl. 1, fig. 2) illustrated this holotype, MCZ 76407, as *Cerion rubicundum viola* (Maynard, 1889).

Holotype Measurements. Length 16.6 mm, diameter (excluding lip) 7.1 mm; aperture height (including lip) 6.4 mm, aperture width (including lip and peristome) 5.2 mm.

Type Locality. Clench (1957: 168) noted "no locality given, but Inagua, Bahamas on original label."

Remarks. Pilsbry and Vanatta (1896: 328) listed this taxon as an undescribed species, whereas Pilsbry (1902: 281) regarded this as an unrecognizable form. Clench (1933: 99) considered this to be a valid species related to *Cerion bryanti* Pfeiffer. Later, Clench (1959, pl. 1, fig. 2) reduced this taxon to a subspecies, *C. rubicundum viola* (Maynard, 1889).

Taxon 24. *Strophia orbicularia* **Maynard, 1889c [October], pl. 16, figs. 6A, B** [no description or mention in text]. Caption to plate 16, figure 6A, "Strophia orbicularia, front view of type; 6B, right side of same."

Type Material. The caption to the figures identified a single type specimen, the holotype. Because no other specimens were mentioned, there are no paratypes. Clench (1959: 45) listed MCZ 76408 and MCZ 76409 as "type specimens." Lot MCZ 76408 is labeled "holotype," closely approximates the illustration, and contains a note in Maynard's hand containing the term "type." This specimen is recognized as the originally designated holotype. The remaining specimen MCZ 76409 is not a paratype because it was not mentioned in the original description.

Holotype Measurements. Length 22.7 mm, diameter (excluding lip) 8.1 mm; aperture height (including lip) 8.1 mm, aperture width (including lip and peristome) 6.2 mm.

Type Locality. Clench (1957: 155) noted "Inagua, Bahamas, label on type specimens."

Remarks. Pilsbry and Vanatta (1896: 328) listed this taxon as an undescribed species. Clench (1933: 99) listed this taxon as a synonym of *Cerion bryanti* Pfeiffer and later (Clench, 1959: 45) of *C.* (*Diacerion*) *rubicundum* (Menke, 1829).

Taxon 25. *Strophia curtissii* **Maynard, 1894a [December]: 107–112, text figs. 33A, B, C, D, fig. 40a** (map). Examined 2,000 specimens. Size of type .98 by .40 [inches; 24.9 by 10.2 mm]. Caption to text figure 33, "Strophia curtissii. . . . B, side view of type; C, front view of same."

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. No specimen was labeled "Holotype" at the MCZ. Lot number MCZ 10274 was labeled "Paratype" and contained two specimens. The smaller of these specimens approximates the published measurements within 3% and more closely resembles figure 33C than 33B. Unlike the remaining specimen (now MCZ 356980), it has a minute lower tooth and lacks an upper tooth, as specified in the description (p. 108). This specimen (MCZ 10274) is here considered to be the

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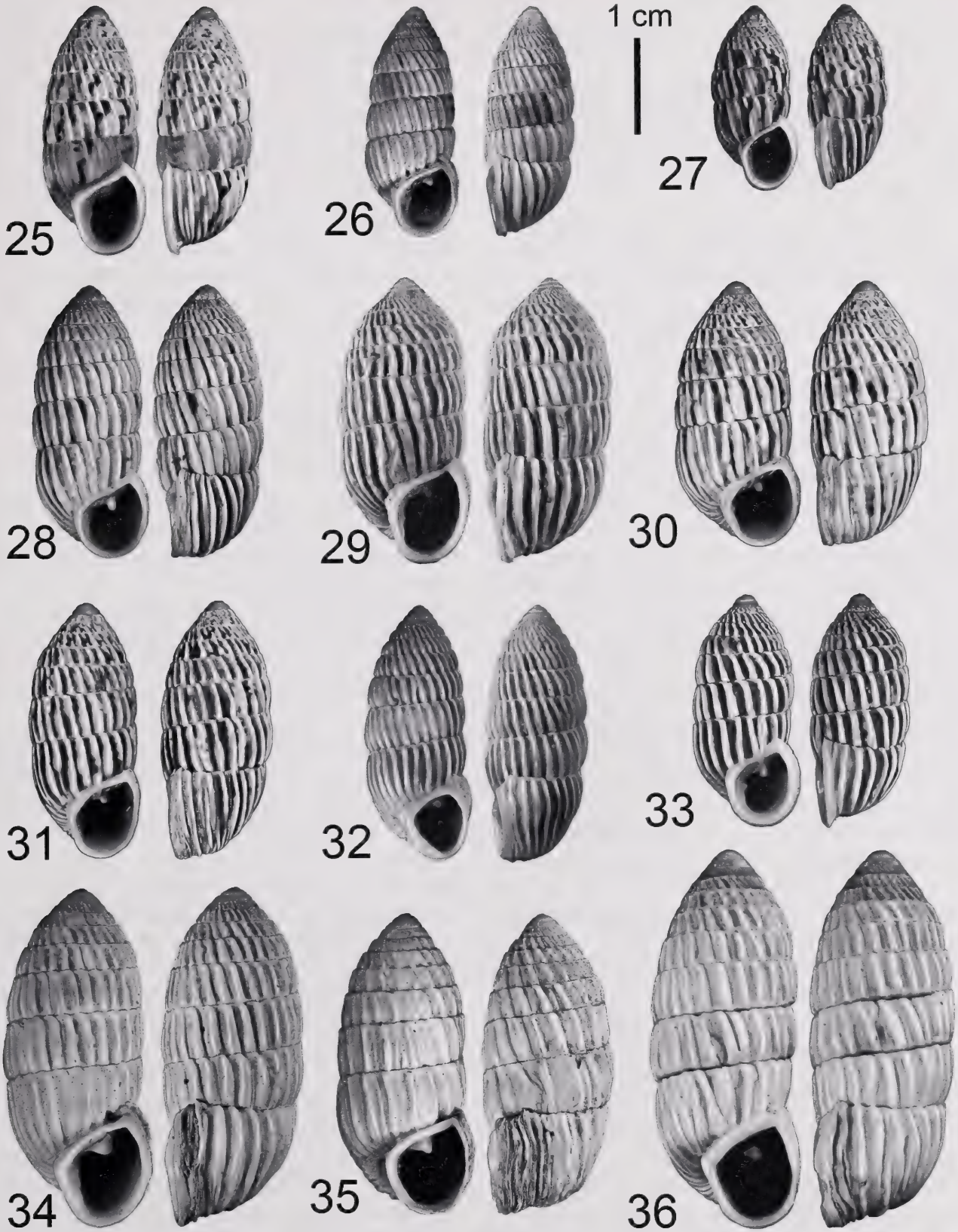
Figures 25–36. Taxon 25. *Strophia curtissii* Maynard, 1894. Holotype MCZ 10274, cemetery east of Nassau, New Providence Island, Bahamas. Taxon 26. *Strophia curtissii nivia* Maynard, 1894. Holotype MCZ 010279. Banyan tree near ruin in the cemetery where *S. curtissii* is found [large cemetery east of Nassau, New Providence Island, Bahamas]. Taxon 27. *Strophia thorndikei* Maynard, 1894. Holotype MCZ 76086. West of main path in cemetery east of Nassau, New Providence Island, Bahamas. Taxon 28. *Strophia cinerea* Maynard, 1894. Holotype MCZ 76254. Hog Island [Paradise Island], along the shore of Middle Bay, on the south side of the Key, New Providence Island, Bahamas. Taxon 29. *Strophia cinerea robusta* Maynard, 1894. Neotype MCZ 356982. North side of Hog Island [Paradise Island], directly back of the beach, New Providence Island, Bahamas. Taxon 30. *Strophia cinerea tracta* Maynard, 1894. Holotype MCZ 76081. Field near the extreme eastern point of Hog Island [Paradise Island], New Providence Island, Bahamas. Taxon 31. *Strophia cinerea mutata* Maynard, 1894. Holotype MCZ 76279. Northern shore of the western half of Long Key, about 1 mile east of Hog Island [Paradise Island], New Providence Island, Bahamas. Taxon 32. *Strophia albea* Maynard, 1894. Holotype MCZ 10242. South side of Spruce Key, due north of Long Key, about 1 mile



east of Hog Island [Paradise Island], New Providence Island, Bahamas. Taxon 33. *Strophia coryi* Maynard, 1894. Holotype MCZ 76079. Along bay on the extreme west end of New Providence Island, Bahamas, also on Spruce Key, N of Long Key, 1 mile east of Hog Island [Paradise Island], New Providence Island, Bahamas. Taxon 34. *Strophia ritchiei* Maynard, 1894. Holotype MCZ 76077. Highburn Key, Exuma Group, Bahamas. Taxon 35. *Strophia grayi* Maynard, 1894. Holotype MCZ 118169. Hill at northern end of Highburn Key, Exuma Group, Bahamas. Taxon 36. *Strophia grayi gigantea* Maynard, 1894. Holotype MCZ 10290, Hillside, middle part of Highburn Key, Exuma Group, Bahamas.

originally designated holotype. How many of the remaining 1,999 specimens are paratypes is uncertain (see Remarks).

Holotype Measurements. Length 25.2 mm, diameter (excluding lip) 9.9 mm; aperture height (including lip) 9.4 mm, aperture width (including lip and peristome) 7.6 mm.

Type Locality. "The type form occurs in the large cemetery to the eastward of Nassau, [New Providence Island, Bahamas] on the western side of a path which crosses the grounds [map, fig. 40a]" (Maynard, 1894a: 109).

Remarks. Maynard (1894a: 109) distinguished five forms [Nos. 1–5] without naming them. The type series is defined (Article 72.4.1, ICZN, 1999: 76) as "all the specimens included by the author in the new nominal taxon, except any that the author expressly excludes from the type series, or refers to as distinct variants (e.g., by name, letter, or number)." Thus, specimens representing forms No. 1–5 are not paratypes of *Strophia curtissii.* Clench (1957: 142) followed Pilsbry (1902: 256) in listing this taxon as a synonym of *Cerion varium* (Bonnet, 1864). Gould and Woodruff (1986: 476) regarded this taxon to be "intermediate" between *Cerion glans* (Küster, 1844) and *C. gubernatorium* (Crosse, 1869).

Taxon 26. *Strophia curtissii nivia* **Maynard, 1894a [December]: 112–116** [*nivea* in text], **fig. 34A** [*nivia* in caption]. Examined 40 specimens. Size of type .90 by .37 [inches; 22.9 by 9.4 mm]. Caption to text figure 34A, "Strophia curtissii nivia, front view of type."

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. How many of the remaining 39 specimens are paratypes is uncertain (see Remarks). An examination of the collections and catalog at the MCZ revealed that, at the time of his death, Maynard's collection contained one lot of this taxon [catalogued as MCZ 76097 "Paratypes"] that contained in excess of 200 specimens, as well as handwritten labels dated 1891 and 1897. These labels indicate that the majority of the specimens were added after the taxon was described. There was no single, segregated specimen labeled "Holotype" either in the collection or the catalog. Lot MCZ 10279 contained two specimens labeled "paratype" and had been purchased from Maynard in 1895. One of these specimens matches the figure of the holotype in having a columellar tooth, which is not evident in the remaining specimen. This specimen is considered to be the holotype. Lot number USNM 420034 contains 100 specimens. Lot number MCZ 10280 contained two specimens labeled "paratype" and are accompanied by a label indicating "Form No. 2," which excludes these specimens from the type series (see Remarks).

Holotype Measurements. Length 23.7 mm, diameter (excluding lip) 9.5 mm; aperture height (including lip) 8.6 mm, aperture width (including lip and peristome) 7.0 mm.

Type Locality. Banyan tree near ruin in the cemetery where *S. curtissii* is found [large cemetery eastward of Nassau, New Providence Island, Bahamas].

Remarks. The taxon name originally appeared as *Strophia curtissii nivea* in the heading of the original description, but as *S. curtissii nivia* in the caption to the figure within the body of the description. Maynard (1913b: 186) described *S. varia-nivia* as "Intermediate between *varia* and *nivia.*" With this use of *nivia,* Maynard (1913b: 186) acted as the First Revisor of spellings [Article 24.2.4, ICZN, 1999: 30–31] and fixed the spelling of this species as *nivia. Strophiops nivia* again appeared in Maynard (1921b: 148) and in Maynard's [1924b?] sales catalog. The spelling "*nivea*" appeared with a citation to the original description in Maynard (1920a: 79). Oddly, Maynard (1913b: 186) described *S. nivia* as a new taxon while incorrectly listing the preceding taxon, *S. varia-nivia* as

previously described. This is almost certainly an error in typesetting. *Strophiops nivia* Maynard (1913) is a junior secondary homonym of *Strophia curtissii nivia* Maynard (1894) as well as an objective junior synonym because they have the same type specimen [see Taxon 72].

Maynard (1894a: 113) distinguished two forms [Nos. 1 and 2] without naming them. The type series is defined in Article 72.4 (ICZN, 1999: 76) as "all the specimens included by the author in the new nominal taxon, . . . except any that the author expressly excludes from the type series, or refers to as distinct variants (e.g., by name, letter, or number)." Thus, specimens representing forms No. 1 or 2 are not paratypes of *Strophia curtissii nivia.* In his discussion of *S. nivia,* Maynard (1921b: 148) provided larger measurements (1.00 by .40 [inches; 25.4 by 10.2 mm]), listed 829 specimens rather than the 40 in the original description, and included citations to illustrations (plate 44, figs. 3, 4) that were never issued.

Clench (1957: 155) listed this taxon as *nivea* and considered *nivia* an error for *nivea.* Gould and Woodruff (1986: 476) regarded this taxon to be "intermediate" between *Cerion glans* (Küster, 1844) and *C. gubernatorium* (Crosse, 1869).

Taxon 27. *Strophia thorndikei* **Maynard, 1894a [December]: 116–119, text figs. 34B, C, D, fig. 40t** (map). Examined 2,000 specimens. Size of type .70 by .30 [inches; 17.8 by 7.6 mm]. Caption to text fig. 34D, "Strophia thorndikei, front view of type."

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. Lot number MCZ 76086 contains a single specimen labeled "Holotype," which is 6% larger than Maynard's published length but otherwise approximates the figure of the type and includes Maynard's original label annotated "type." This specimen is here recognized as the Holotype. Lot number USNM 419958 contains 200 paratypes. How many of the remaining 1,799 specimens, are paratypes is uncertain (see Remarks).

Holotype Measurements. Length 18.9 mm, diameter (excluding lip) 8.1 mm; aperture height (including lip) 7.9 mm, aperture width (including lip and peristome) 6.2 mm.

Type Locality. West of main path in cemetery eastward of Nassau (map, fig. 40t) [New Providence Island, Bahamas].

Remarks. Maynard (1894a: 117–118) distinguished five forms [Nos. 1–5] without naming them. He illustrated form No. 3 (fig. 34B) and form No. 4 (fig. 34C). Specimens representing forms No. 1–5 are not paratypes of *Strophia thorndikei* [Article 72.4, ICZN, 1999: 76]. This taxon was figured by Manard (1919b: 47, fig. 8 as *S. thorndikeii* Mayn.). Maynard (1921b: 146) provided descriptive notes, including reference to a color illustration (plate 8, fig. 10) published in 1919, and commented that the taxon was represented by 2,500 specimens, at least 500 of which presumably were collected after the taxon was described. Maynard (1924c: 6) listed *S. thorndikei* as extinct in 1913 because of burning of vegetation prior to cultivation. Gould and Woodruff (1986: 476) regarded this taxon to be "intermediate" between *Cerion glans* (Küster, 1844) and *C. gubernatorium* (Crosse, 1869).

Taxon 28. *Strophia cinerea* **Maynard, 1894a [December]: 119–121, text figs. 35A, B, fig. 40e** (map). Examined 2,000 specimens. Size of type 1.15 by .45 [inches; 29.2 by 11.4 mm]. Caption to text figure 35, "B, front view of type. A, side view of same."

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. Lot number MCZ 76254 contains a single specimen labeled "Holotype," which is within 5% of the published measurements and includes Maynard's original

label annotated "type." This specimen is here recognized as the Holotype. Lot number USNM 420076 contains 200 paratypes. How many of the remaining 1,799 specimens are paratypes is uncertain (see Remarks).

Holotype Measurements. Length 28.0 mm, diameter (excluding lip) 11.3 mm; aperture height (including lip) 9.4 mm, aperture width (including lip and peristome) 7.6 mm.

Type Locality. Hog Island [Paradise Island], along the shore of Middle Bay, on the south side of the key (map, fig. 40e) [New Providence Island, Bahamas].

Remarks. Maynard (1894a: 120–121) distinguished three forms [Nos. 1–3] without naming them. Specimens representing forms No. 1–3 are not paratypes of *Strophia cinerea* [Article 72.4, ICZN, 1999: 76]. Maynard (1921b: 144; 1925, pl. 40, figs. 3, 4) noted 2,500 specimens, which must have included subsequent collections, and provided new, colored illustrations for this taxon.

Taxon 29. *Strophia cinerea robusta* **Maynard, 1894a [December]: 121–123, text figs. 36 A, B, fig. 40f** (map). Examined 75 specimens. Size of type 1.12 by .55 [inches; 28.4 by 14.0 mm]. Caption to text figure 36, "Strophia cinerea robusta. A, front view, B, side view, of type."

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. There is no specimen labeled "Holotype" at the MCZ. An examination of the MCZ catalog showed that no representatives of this taxon were present in Maynard's collection when purchased from his daughter. Lot number MCZ 10259 was labeled "Paratype" and contained two specimens that were acquired from Maynard in 1895. The specimen in MCZ 10259 that more closely matches the published figures and measurements was recatalogued as MCZ 356982 and is here designated as the neotype. How many of the remaining 74 specimens are paratypes is uncertain (see Remarks).

Neotype Measurements. Length 29.0 mm, diameter (excluding lip) 13.0 mm; aperture height (including lip) 11.3 mm, aperture width (including lip and peristome) 8.4 mm.

Type Locality. North side of Hog Island [Paradise Island], directly back of the beach (map, fig. 40f) [New Providence Island, Bahamas].

Remarks. Maynard (1894a: 123) distinguished a small form [No. 1] without naming it. Lot MCZ 10260 contained two specimens labeled form No. 1. Specimens representing this form are not paratypes of *Strophia cinerea robusta* [Article 72.4, ICZN, 1999: 76]. Gould and Woodruff (1986: 475) regarded this taxon to be a synonym of *Cerion glans* (Küster, 1844).

Taxon 30. *Strophia cinerea tracta* **Maynard, 1894a [December]: 123–125, text fig. 37A, fig. 40g** (map). Examined 300 specimens. Size of type 1.05 by .45 [inches; 26.7 by 11.4 mm]. Caption to text figure 37A, "Strophia cinerea tracta, front view of type."

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. Lot number MCZ 76081 contains a single specimen labeled "Holotype," closely matches Maynard's published length and figure of the type, and includes Maynard's original label annotated "type." This specimen is here recognized as the Holotype. Lot number USNM 420042 contains paratypes. How many of the remaining specimens are paratypes is uncertain (see Remarks).

Holotype Measurements. Length 26.9 mm, diameter (excluding lip) 12.0 mm; aperture height (including lip) 9.6 mm, aperture width (including lip and peristome) 8.4 mm.

Type Locality. Field near the extreme eastern point of Hog Island [Paradise Is-

land] (map, fig. 40g) [New Providence Island, Bahamas].

Remarks. Maynard (1894a: 124–125) distinguished five forms [Nos. 1–5] without naming them. Specimens representing forms No. 1–5 are not paratypes of *Strophia cinerea tracta* [Article 72.4, ICZN, 1999: 76]. Maynard (1921b: 144–145) listed this taxon as a full species, and provided new, colored illustrations (Maynard, 1925, pls. 40, figs. 7, 8). Clench (1957: 165) followed Pilsbry (1902: 253) in synonymizing this taxon under *Cerion varium* (Bonnet, 1864), whereas Gould and Woodruff (1986: 475) considered it to be a synonym of *C. glans* (Küster, 1844).

Taxon 31. *Strophia cinerea mutata* **Maynard, 1894a [December]: 125–128, text fig. 37B, fig. 40h** (map). Examined 100 specimens. Size of type 1.15 by .40 [inches; 29.2 by 10.2 mm]. Caption to text figure 37B, "Strophia cinerea mutata, front view of type."

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. Lot number MCZ 76279 contains a single specimen labeled "Holotype," which is 11% shorter than Maynard's published length and slightly wider but approximates the figure of the type and contains Maynard's original label annotated "type." This specimen is here recognized as the Holotype. Lot number USNM 420132 contains paratypes. How many of the remaining specimens are paratypes is uncertain (see Remarks).

Holotype Measurements. Length 26.0 mm, diameter (excluding lip) 11.0 mm; aperture height (including lip) 9.7 mm, aperture width (including lip and peristome) 8.0 mm.

Type Locality. Northern shore of the western half of Long Key, about 1 mile east of Hog Island [Paradise Island] (map, fig. 40h) [New Providence Island, Bahamas].

Remarks. Maynard (1894a: 126) distinguished a single form [No. 1] without naming it. Specimens representing this form are not paratypes of *Strophia cinerea mutata* [Article 72.4, ICZN, 1999: 76]. Maynard (1921b: 146) listed this taxon as a full species and referred to a previously published [1920a, pl. 10*, fig. 4] colored illustration but noted a different locality (Atoll Island) and a higher number of specimens (200).

Taxon 32. *Strophia albea* **Maynard, 1894a [December]: 128–129, text figs. 38A, B.** Examined 40 specimens [only three living specimens]. Size of type 1.00 by .36 [inches; 25.4 by 9.1 mm]. Caption to text figure 38, "Strophia albea. A, front view, B, side view, of type."

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. The remaining 39 specimens are paratypes. No specimen was labeled "Holotype" at the MCZ. An examination of the MCZ catalog showed that no representatives of this taxon were present in Maynard's collection when purchased from his daughter. Lot MCZ 10242 was labeled "Paratype" and contained two specimens that were acquired from Maynard in 1895. One of these specimens approximates the length in the original description to within 3% and agrees with the generalized illustration (more fig. 38B than 38A). This specimen is considered to be the Holotype. The remaining specimen has been recatalogued as MCZ 356983. Maynard (1921b: 139) listed 590 specimens, indicating that 550 specimens had been added. Some of the 100 specimens of USNM 420097 may be paratypes.

Holotype Measurements. Length 26.0 mm, diameter (excluding lip) 10.1 mm; aperture height (including lip) 9.0 mm, aperture width (including lip and peristome) 6.8 mm.

Type Locality. South side of Spruce Key, due north of Long Key, about 1 mile E of

Hog Island [Paradise Island] [New Providence Island, Bahamas].

Remarks. The identical illustration appears in Maynard (1913c: 200) as *Strophiops albea* Mayn. and again in a colored version (Maynard, 1919c, pl. 10, figs. 1, 2 [lower row]). The taxon was redescribed in Maynard (1921b: 139) on the basis of examination of 590 specimens. It appeared twice in the sales catalog (Maynard, 1924b: [6] and [7]), the first time correctly (from Spruce Key), the second time from Rum Key, an error for *alba.* Clench (1957: 165) followed Pilsbry (1902: 253) in synonymizing this taxon under *Ceron varium* Bonnet, 1864. Gould and Woodruff (1986: 474) had examined "paratypes" (presumably MCZ 10242) and synonymized this taxon with *C. glans* (Küster, 1844).

Taxon 33. *Strophia coryi* **Maynard, 1894a [December]: 129–135, text figs. 39A, B.** Examined 2,000 specimens. Size of type 1.00 by .40 [inches; 25.4 by 10.2 mm]. Caption to text figure 39, "Strophia coryi, A, front view, B, side view, of type." The same figures appear (Maynard, 1913c: 200) as *Strophiops coryi* Mayn.

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. Clench (1934: 214) mentioned examining type specimens but did not further identify them. Lot number MCZ 76079 contains a single specimen labeled "Holotype," which is 6% shorter and slightly wider than Maynard's published measurements but approximates the figure of the type and contains Maynard's original label annotated "type." This specimen is here recognized as the Holotype. Lot number USNM 419983 contains 100 paratypes. How many of the remaining 1,899 specimens are paratypes is uncertain (see Remarks).

Holotype Measurements. Length 23.9 mm, diameter (excluding lip) 10.4 mm; aperture height (including lip) 9.2 mm, aperture width (including lip and peristome) 7.9 mm.

Type Locality. Along bay on the extreme west end of New Providence Island, Bahamas, also on Spruce Key, N of Long Key, 1 mile E of Hog Island [Paradise Island] [New Providence Island, Bahamas].

Remarks. Maynard (1894a: 131–132) distinguished five forms [Nos. 1–5] without naming them. Specimens representing forms No. 1–5 are not paratypes of *Strophia coryi* [Article 72.4, ICZN, 1999: 76]. This taxon was subsequently reillustrated (Maynard, 1919b, fig. 18, pl. 7, figs. 9, 10). Clench (1934: 214, 1952: 108) listed this taxon as a form of *Cerion glans* (Küster, 1844).

Taxon 34. *Strophia ritchiei* **Maynard, 1894a [December]: 135–138, text figs. 41A, B.** Examined 1,000 specimens. Size of type 1.37 by .57 [inches; 34.5 by 14.5 mm]. Caption to text figure 41, "Strophia ritchiei, A, front; B, side view of type." [Illustration repeated on back cover of Maynard (1913) and the front covers of Maynard (1920a–1924a) as *Strophiops ritchiei* Mayn.]

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. Lot number MCZ 76077 contains a single specimen labeled "Holotype," which is within 0.1 mm of Maynard's published measurements, approximates the figure of the type, and contains Maynard's original label annotated "type." This specimen is here recognized as the Holotype. Lot number USNM 419967 contains 500 paratypes. How many of the remaining 499 specimens are paratypes is uncertain (see Remarks).

Holotype Measurements. Length 34.6 mm, diameter (excluding lip) 14.6 mm; aperture height (including lip) 13.17 mm, aperture width (including lip and peristome) 10.12 mm.

Type Locality. Highburn Key [Exuma Group, Bahamas].

Remarks. Maynard (1894a: 136–137) distinguished four forms [Nos. 1–4] without naming them. Specimens representing forms No. 1–4 are not paratypes of *Strophia ritchiei* [Article 72.4, ICZN, 1999: 76]. The name was misspelled as *S. ritchei* (Maynard, 1920a: 75).

Taxon 35. *Strophia grayi* **Maynard, 1894a [December]: 138–141, text figs. 42A, B.** Examined 700 specimens. Size of type 1.25 by .47 [inches; 31.8 by 17.8 mm]. Caption to text figure 42, "Strophia grayi, A, front; B, side view of type."

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. Lot number MCZ 118169 contains a single specimen labeled "co-type." This specimen approximates the published length (within 5%) and is a reasonable approximation of the original illustration. It is accompanied by a label identifying it as a co-type, initialed by Maynard and dated "12/14/15," indicating that the label was added after the description of the species. This specimen is here recognized as the Holotype. Lot number USNM 420101 contains 100 paratypes. How many of the remaining 599 specimens are paratypes is uncertain (see Remarks).

Holotype Measurements. Length 30.5 mm, diameter (excluding lip) 13.0 mm; aperture height (including lip) 11.0 mm, aperture width (including lip and peristome) 9.1 mm.

Type Locality. Hill at northern end of Highburn Key [Exuma Group], Bahamas.

Remarks. Maynard (1894a: 139–141) distinguished three forms [Nos. 1–3] without naming them and illustrated form No. 3 (fig. 43A). Specimens representing forms No. 1–3 are not paratypes of *Strophia grayi* [Article 72.4, ICZN, 1999: 76].

Taxon 36. *Strophia grayi gigantea* **Maynard, 1894a [December]: 141–143, text fig. 44A.** Examined 50 specimens. Size of type 1.56 by .55 [inches; 39.6 by 14.0 mm]. Caption to text figure 44A, "Strophia grayi gigantea."

Type Material. The original description provided measurements for a single "type" specimen, but the illustrated specimen was not referred to as type. The measurements are considered to designate a holotype. No specimen labeled holotype could be found at the MCZ. Two specimens of MCZ 10290 were labeled "paratype." The larger of these specimens approximates the length and width in the original description to within 4%. This specimen is considered to be the Holotype. The remaining specimen (now MCZ 356984) is a paratype. How many of the remaining 48 specimens are paratypes is uncertain (see Remarks).

Holotype Measurements. Length 38.1 mm, diameter (excluding lip) 14.4 mm; aperture height (including lip) 12.6 mm, aperture width (including lip and peristome) 9.9 mm.

Type Locality. Hillside, middle part of Highburn Key [Exuma Group], Bahamas.

Remarks. Maynard (1894a: 139–141) distinguished a single form [No. 1] without naming it. Two specimens of MCZ 10291 were labeled "paratype." However, Maynard's printed label, which accompanies these two specimens, identifies them as form No. 1. Specimens representing this form are not paratypes of *Strophia grayi gigantea* [Article 72.4.1, ICZN, 1999: 76].

Taxon 37. *Strophia grayi pumilia* **Maynard, 1894a [December]: 143–144, text fig. 44B.** Examined 50 specimens. Size of type .90 by .42 [inches; 22.9 by 10.7 mm]. Caption to text figure 44B, "Strophia grayi pumilia."

Type Material. The original description provided measurements for a single "type" specimen, but the illustrated specimen was not referred to as a type. The measurements are sufficient to designate a holotype. No specimen was labeled "Holotype" at the MCZ. The MCZ collections contain two lots of *Strophia grayi pumilia,* both

labeled "paratype." One, MCZ 76325, contains 12 specimens, the other, MCZ 10292, contains two specimens. Although none match the measurements precisely, the larger of the two specimens in MCZ 10292 comes closest to approximating the size (within 5%) and proportions (within 1%) of the measurements as well as the illustration. This specimen is regarded as the originally designated Holotype, the remaining specimen (now MCZ 356985) is a paratype. The remaining 48 specimens are paratypes.

Holotype Measurements. Length 23.7 mm, diameter (excluding lip) 11.1 mm; aperture height (including lip) 8.9 mm, aperture width (including lip and peristome) 7.9 mm.

Type Locality. South of deep gorge, middle part of Highburn Key [Exuma Group], Bahamas.

Remarks. The taxon appeared as "Strophia gray! pumilia" in the original description and as *Strophia grayi pumilia* in the figure caption but as *pumilla* in the index.

Taxon 38. *Strophia eburnia* **Maynard, 1894a [December]: 144–148** [pages printed out of order], **text figs. 45A, B.** Examined 100 specimens [12 collected living, p. 147]. Size of type 1.15 by .45 [inches; 29.2 by 11.4 mm]. Caption to text figure 45, "Strophia eburnia, A, front view, B, side view of type."

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. The remaining 99 specimens are paratypes. Lot MCZ 76224 was labeled "syntypes" and contained two specimens, as well as Maynard's original label annotated "type." One specimen is gray, has a red "Holotype" label affixed to it, and conforms to the published figure as well as the measurements given for "the type." The original catalog entry at the MCZ listed only one specimen and referred to it as the "holotype." The gray, labeled specimen is here recognized as the holotype. The other dark brown specimen is a paratype and has been recatalogued as MCZ 356986. Lot USNM 420021 contains 30 paratypes.

Holotype Measurements. Length 29.0 mm, diameter (excluding lip) 11.2 mm; aperture height (including lip) 9.9 mm, aperture width (including lip and peristome) 8.3 mm.

Type Locality. U Key [Exuma Group], Bahamas, single specimen tentatively identified as this species on Pimlico Key.

Remarks. This taxon was misspelled as *S. eburnea* (Maynard, 1920a: 74, 78).

Taxon 39. *Strophia elongata* **Maynard, 1894a [December]: 148–150** [pages printed out of order], **text figs. 46A, B.** Examined 25 specimens. Size of type 1.33 by .50 [inches; 33.8 by 12.7 mm]. Caption to text figure 46, "Strophia elongata, A, front B, side view."

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. The remaining 24 specimens are paratypes. There are no specimens of *S. elongata* in the collections of the MCZ, nor were there any entries corresponding to this taxon in the MCZ catalog either during Maynard's life or among the specimens purchased from his estate. Although it seems probable that Maynard retained the holotype in his collection, it might not

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Figures 37–48. Taxon 37. *Strophia grayi pumilia* Maynard, 1894. Holotype MCZ 10292. South of deep gorge, middle part of Highburn Key, Exuma Group, Bahamas. Taxon 38. *Strophia eburnia* Maynard, 1894. Holotype MCZ 76224. U Key, Exuma Group, Bahamas. Taxon 39. *Strophia elongata* Maynard, 1894. Neotype FMNH 42208. Key, 1 mile north of U Key at Allen's Harbor, Exuma Group, Bahamas. Taxon 40. *Strophia neglecta* Maynard, 1894. Holotype MCZ 76376. One mile west of Fort Charlotte, New Providence Island, Bahamas. Taxon 41. *Strophia neglecta agava* Maynard, 1894. Holotype MCZ 76103. Sisal fields west of Nassau, New Providence Island, Bahamas. Taxon 42. *Strophia carlotta* Maynard, 1894. Holotype MCZ 10249. At the foot of the hill (north side) on which stands Fort Charlotte, New Providence Island, Bahamas. Taxon 43. *Strophia glans*

grisea Maynard, 1894. Holotype MCZ 356674. Fields north of Fresh Creek, about 1 mile from the settlement, Andros, Bahamas. Taxon 44. *Strophia regula* Maynard, 1894. Neotype MCZ 10299. Fields on both sides of Fresh Creek, near the settlement, Andros, Bahamas. Taxon 45. *Strophia bimarginata* Maynard, 1894. Neotype USNM 420095. Green Key, east coast of Andros, Bahamas. Taxon 46. *Strophia bimarginata cera* Maynard, 1894. Holotype MCZ 76379. Green Key, east coast of Andros, Bahamas. Taxon 47. *Strophia pilsbryi* Maynard, 1894. Holotype MCZ 10297. Eastern half of Goat Key, Middle Bight, Andros, Bahamas. Taxon 48. *Strophia pilsbryi evolva* Maynard, 1894. Holotype MCZ 76383. Western end of Goat Key, Middle Bight, Andros, Bahamas.

have been labeled prominently. At least some specimens of this taxon would have been retained at the MCZ had they been recognizably labeled in Maynard's collection. Nor was this taxon present among the material sent to USNM after the acquisition of Maynard's collection. The Field Museum of Natural History has two specimens (FMNH 42208) that were collected by Maynard in 1893 and are paratypes. Because the holotype is clearly lost, the better preserved FMNH specimen, which also more closely approximates the measurements and illustration, is designated as the neotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. This neotype retains FMNH 42208, whereas the remaining specimen, a paratype, was recatalogued as FMNH 303191.

Neotype Measurements. Length 34.3 mm, diameter (excluding lip) 12.2 mm; aperture height (including lip) 11.2 mm, aperture width (including lip and peristome) 8.7 mm.

Type Locality. Key, 1 mile north of U Key at Allen's Harbor [Exuma Group], Bahamas.

Remarks. Maynard (1894a: 149) noted that no living specimens were found, and commented that the site had been inhabited by Lucayan Indians.

Taxon 40. *Strophia neglecta* **Maynard, 1894a [December]: 148–150** [pages printed out of order], **text figs. 46A, B.** Number of examined specimens not provided. Size of type .92 by .45 [inches; 23.4 by 11.4 mm]. Caption to text figure 45, "Strophia neglecta, A, front view, B, side view of type."

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. Although the number of specimens examined was not mentioned in the description, Maynard (1894a: 151) discussed variation in this taxon and noted that they were abundant and that "all gathered in this locality were typical." MCZ 76376 contains a single specimen labeled "Holotype" that approximates the measurements and illustration of this taxon and is accompanied by a label in Maynard's hand with the term "type" that includes references to figures published after this species was described. This specimen is here recognized as the holotype.

Holotype Measurements. Length 22.60 mm, diameter (excluding lip) 11.2 mm; aperture height (including lip) 9.32 mm, aperture width (including lip and peristome) 8.44 mm.

Type Locality. One mile west of Fort Charlotte, New Providence Island, Bahamas.

Remarks. Maynard (1894a: 151–152) commented that the field had been converted to agave cultivation and that after 9 years, *S. neglecta* "no longer exists," having been replaced by *S. neglecta agava.* This taxon was illustrated as *Strophiops neglecta* (Maynard, 1913a: 177, 1919a: 4, fig. 3, pl. 5, figs. 4, 5). Maynard (1921b: 142) gave the number of specimens as 500 and commented that it was probably extinct. Maynard (1924c: 6) listed *S. neglecta* as extinct in 1913 from the burning of vegetation prior to cultivation.

Taxon 41. *Strophia neglecta agava* **Maynard, 1894a [December]: 152, 1894b [December]: 153–154, text figs. 48A, B.** Examined 500 specimens. Size of type as 1.21 by .47 [inches; 30.7 by 17.8 mm]. Caption to text figure 48, "Strophia neglecta agava, A, front, B, side view of type."

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. Lot MCZ 76103, which is labeled "Holotype" and contains a single specimen accompanied by a note in Maynard's handwriting with the term "type," is here recognized as the Holotype (despite the 5% difference in length). The remaining 499

specimens, including MCZ 76104 and MCZ 10296, are paratypes.

Holotype Measurements. Length 29.2 mm, diameter (excluding lip) 12.6 mm; aperture height (including lip) 11.7 mm, aperture width (including lip and peristome) 9.6 mm.

Type Locality. Sisal fields west of Nassau, New Providence Island, Bahamas.

Remarks. Originally proposed as a subspecies, this taxon was elevated to a full species by Maynard (1913c: 191). The original illustration was subsequently republished as *Strophiops agava* (Maynard, 1913c: 200, 1919c, fig. 24, 1920c: 104, fig. 87, pl. 19, fig. 20 [apertural view only]). Clench (1957: 136) considered this taxon to be a synonym of *Cerion coryi* (Maynard, 1894). Gould and Woodruff (1986: 474) had examined the holotype and synonymized it with *C. glans* (Küster, 1844).

Taxon 42. *Strophia carlotta* **Maynard, 1894b [December]: 154–156, text figs. 49A, B.** Examined 1,000 specimens. Size of type .85 by .40 [inches; 21.6 by 10.2 mm]. Caption to text figure 49, "Strophia carlotta, A, front, B, side view of type."

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. How many of the remaining 999 specimens are paratypes is uncertain (see Remarks). Lot MCZ 10249 was labeled "paratype" and contained two specimens that were acquired from Maynard in 1895. One of these specimens closely resembles the illustration, but both length and width are exactly 1 mm longer than the published measurements. This specimen is considered to be the figured specimen and the originally designated holotype. The remaining specimen, a paratype, was recatalogued as MCZ 356987. There were no MCZ catalog entries for this taxon in the material from Maynard's estate.

Holotype Measurements. Length 22.6 mm, diameter (excluding lip) 11.2 mm; aperture height (including lip) 8.7 mm, aperture width (including lip and peristome) 7.6 mm.

Type Locality. At the foot of the hill (north side) on which stands Fort Charlotte, New Providence Island, Bahamas.

Remarks. Maynard (1894b: 156) distinguished two forms [Nos. 1 and 2] without naming them. Two specimens of MCZ 10250 are labeled form No. 1, whereas MCZ 10251 contains four specimens labeled form No. 2. Specimens representing forms No. 1 and 2 are not paratypes of *Strophia carlotta* [Article 72.4, ICZN, 1999: 76]. Maynard (1913c: 192) recognized that this is a synonym of *S. glans* (Küster, 1844), as did Gould and Woodruff (1986: 474).

Taxon 43. *Strophia glans grisea* **Maynard, 1894b [December]: 159–161, text figs. 51A, B.** Examined 200 specimens. Size of type 1.10 by .45 [inches; 27.9 by 11.4 mm]. Caption to text figure 48, "Strophia glans grisea, A, front view of type, B, margin of same."

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. A search of the MCZ catalog indicated that only one lot containing 222 specimens was present in Maynard's collection at the time it was acquired from his daughter. This lot, MCZ 76085, was catalogued as "paratypes" and did not contain a label in Maynard's handwriting. These specimens were compared against the published measurements and illustration. Although none matched exactly, a single specimen was identified that most closely approximated the figures and measurements. This specimen is considered to be the originally designated holotype and has been recatalogued as MCZ 356674.

Holotype Measurements. Length 27.3 mm, diameter (excluding lip) 11.6 mm; aperture height (including lip) 11.2 mm, aperture width (including lip and peristome) 9.6 mm.

Type Locality. Fields north of Fresh Creek, about 1 mile from the settlement Andros, Bahamas.

Remarks. Maynard (1894b: 161) noted that this taxon was also found south of the creek and that these specimens "were undoubtedly transplanted from the north side through the agency of the inhabitants, who pass from one set of fields to the other, carrying with them the plants of the casava on which the Strophias frequently occur."

Taxon 44. *Strophia regula* **Maynard, 1894b [December]: 161–164, text figs. 52A, B.** Examined 50 specimens. Size of type 1.50 by .60 [inches; 38.1 by 15.2 mm]. Caption to text figure 52, "Regular Strophia. A, side, B, front view of type."

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. The remaining 49 specimens are paratypes. A review of the MCZ catalog revealed that Maynard's collection contained one lot of 25+ specimens [MCZ 76381] that had been catalogued as "paratypes." Neither this lot nor any single specimen identified as the holotype could be found at the MCZ. Lot MCZ 10299 contained two specimens labeled "paratype" that had been purchased from Maynard in 1895. Both specimens have damage, indicating they had been occupied by hermit crabs, but neither closely matched the figure or published measurements of the holotype. The less damaged specimen retains MCZ 10299 and is here designated as the neotype of *Strophia regula* to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of it. The remaining specimen, a paratype, has been recatalogued as MCZ 356988.

Neotype Measurements. Length 33.3 mm, diameter (excluding lip) 14.4 mm; aperture height (including lip) 12.5 mm, aperture width (including lip and peristome) 10.5 mm.

Type Locality. Fields on both sides of Fresh Creek, near the settlement Andros, Bahamas.

Remarks. Maynard (1894b: 162) reported that this taxon is known only from shells inhabited by hermit crabs and suggested that the species is extinct. Maynard (1919c: 68, caption to fig. 30*, 1921a: 131, 1924?: [7]) referred to this taxon as *S. regular.*

Taxon 45. *Strophia bimarginata* **Maynard, 1894b [December]: 164–168, text figs. 53A, B, C, D.** Examined 2,000 specimens. Size of type 1.50 by .60 [inches; 38.1 by 15.2 mm]. Caption to text figure 53, "Strophia bimarginata. A, front view; B, side view of type."

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. How many of the remaining 1,999 specimens are paratypes is uncertain (see Remarks). No specimen labeled holotype could be found at the MCZ. Lot MCZ 10246 contains two specimens labeled "paratype." Neither of these specimens matches the measurements nor has the "double margin" evident in figure 53B. The holotype is presumed to be lost. Lot USNM 420095 contains over 200 paratypes. A specimen that closely approximates the measurements and the published figures is here designated as neotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of this taxon. This specimen retains USNM 420095. The remaining paratypes have been recatalogued under USNM 1093843. Other paratypes include MCZ 76105 (202 specimens), MCZ 10244 (two specimens), and MCZ 10245 (two specimens).

Neotype Measurements. Length 27.5 mm, diameter (excluding lip) 11.4 mm; aperture height (including lip) 8.9 mm, aperture width (including lip and peristome) 7.4 mm.

Type Locality. Green Key, east coast of Andros, Bahamas.

Remarks. Maynard (1894b: 167) distinguished two forms [Nos. 1 and 2] without naming them. He reported that form No. 1 also occurs on Little Galden Key. Specimens representing forms No. 1 and 2 are not paratypes of *Strophia bimarginata* [Article 72.4, ICZN, 1999: 76].

Taxon 46. *Strophia bimarginata cera* **Maynard, 1894b [December]: 168–170, text figs. 54A, B.** Examined nine specimens. Size of type 1.00 by .40 [inches; 25.4 by 10.2 mm]. Caption to text figure 54, "Strophia bimarginata cera. A, front [sic, margin]; B, margin [sic, front] of type."

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. Lot MCZ 76379, which is labeled "Holotype" and contains a single specimen accompanied by a note in Maynard's handwriting with the term "type," is here recognized as the holotype. The remaining eight specimens, including MCZ 76380 and MCZ 10248, are paratypes.

Holotype Measurements. Length 24.8 mm, diameter (excluding lip) 10.5 mm; aperture height (including lip) 9.1 mm, aperture width (including lip and peristome) 7.0 mm.

Type Locality. Green Key, east coast of Andros, Bahamas.

Taxon 47. *Strophia pilsbryi* **Maynard, 1894b [December]: 170–172, text figs. 55A, B, text fig. 56** (map). Examined 125 specimens. Size of type as 1.07 by .45 [inches; 27.2 by 11.4 mm]. Caption to text figure 55, "Strophia pilsbryi. A, front, B, side view, of type."

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. The remaining 124 specimens are paratypes. No specimen labeled holotype could be found at the MCZ. Lot MCZ 10297 contained two specimens labeled "paratypes" that had been obtained from Maynard in 1895. One of these specimens very closely matches the published measurements and figures of the holotype. This specimen is considered to be the originally designated holotype. The other specimen has been recatalogued as MCZ 356989.

Holotype Measurements. Length 27.3 mm, diameter (excluding lip) 11.4 mm; aperture height (including lip) 10.1 mm, aperture width (including lip and peristome) 8.8 mm.

Type Locality. Eastern half of Goat Key, Middle Bight, Andros, Bahamas (map, fig. 56, †).

Remarks. Maynard (1894b: 171) discussed a single form but did not distinguish it with either a name or number.

Taxon 48. *Strophia pilsbryi evolva* **Maynard, 1894b [December]: 173–175, text figs. 57A, B, C.** Examined 70 specimens. Size of type 1.12 by .43 [inches; 28.4 by 10.9 mm]. Caption to text figure 5, "Strophia pilsbryi evolva. A, front view, B, side view of type."

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. Lot MCZ 76383 contains a single specimen labeled "Holotype" that closely approximates the illustration and the measurements of this taxon. This specimen is recognized as the holotype. The remaining 69 specimens are paratypes.

Holotype Measurements. Length 28.4 mm, diameter (excluding lip) 11.5 mm; aperture height (including lip) 10.7 mm, aperture width (including lip and peristome) 9.0 mm.

Type Locality. Western end of Goat Key, Middle Bight, Andros, Bahamas (map, fig. 56,*).

Taxon 49. *Strophia restricta* **Maynard, 1894b [December]: 175–177, text figs. 58A, B** (map, p. 172, fig. 56). Examined 75 specimens. Size of type .75 by .32 [inches; 19.1 by 8.1 mm]. Caption

to text figure 58, "Strophia restricta. A, front, B, side view."

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. There is no specimen at the MCZ labeled "holotype." MCZ 76384 contained 33 specimens and labels stating "paratype," as well as six handwritten labels, seemingly by Maynard. All bear the taxon name, one contains the term "types," the remainder are numbered 1, 3, 4, 5, 7. None of the specimens match the published measurements. However, neither do the published illustrations. The specimen most closely resembling the measurements, figures, and proportions is considered to be the Holotype. The remaining 32 specimens have been recatalogued as MCZ 356990.

Holotype Measurements. Length 20.2 mm, diameter (excluding lip) 9.3 mm; aperture height (including lip) 7.4 mm, aperture width (including lip and peristome) 6.6 mm.

Type Locality. Western end of Goat Key, Middle Bight, Andros, Bahamas (Maynard, 1894b, fig. 56, ‡).

Remarks. Maynard (1894b: 177) reported that this taxon was "confined to a single tree and the bushes that come in contact with it." Maynard (1894b: 176) distinguished a single form [No. 1] without naming it. Specimens representing this form [No. 1] are not paratypes of *Strophia restricta* [Article 72.4, ICZN, 1999: 76]. Two specimens of MCZ 10301 are labeled form No. 1 and therefore are not paratypes.

Taxon 50. *Strophia eximea* **Maynard, 1894b [December]: 177–179, text figs. 59A, B, 61A, B.** Examined 1,000 specimens. Size of type as 1.12 by .45 [inches; 28.5 by 12.8 mm]. Caption to text figure 59, "Strophia eximia. A, front, B, side view of type."

Type Material. The original description provided measurements for a single "type" specimen, the holotype, which was illustrated. Lot MCZ 76243 contains a single specimen labeled "Holotype" and closely approximates the published measurements and figure. A scrap of cardboard labeled "type" by Maynard accompanies this specimen, which is here recognized as the holotype. Lot USNM 420038 contains 15 paratypes. How many of the remaining 984 specimens are paratypes is uncertain (see Remarks).

Holotype Measurements. Length 28.8 mm, diameter (excluding lip) 11.3 mm; aperture height (including lip) 11.1 mm, aperture width (including lip and peristome) 8.9 mm.

Type Locality. "Procured by Mr. Curtiss in Nassau, from a creole who brought them from Cat Island."

Remarks. Maynard (1894b: 179) distinguished a single form [No. 1] without naming it. Specimens representing this form [No. 1] are not paratypes of *Strophia eximea* [Article 72.4, ICZN, 1999: 76]. This taxon serves as the type species of the genus *Multistrophia* Maynard, (1894b: 179) and is later (Maynard, 1920a: 69, 1920d: 126) included within *Multicostata* (likely errors for *Multistrophia*).

Taxon 51. *Strophia agrestina* **Maynard, 1894b [December]: 179–182, text figs. 60A, B, C.** Examined 1,000 specimens. Size of type .87 by .35 [inches; 22.1 by 8.9 mm]. Caption to text figure 60, "Strophia agristina. A, front, B, side view of type."

Type Material. The original description

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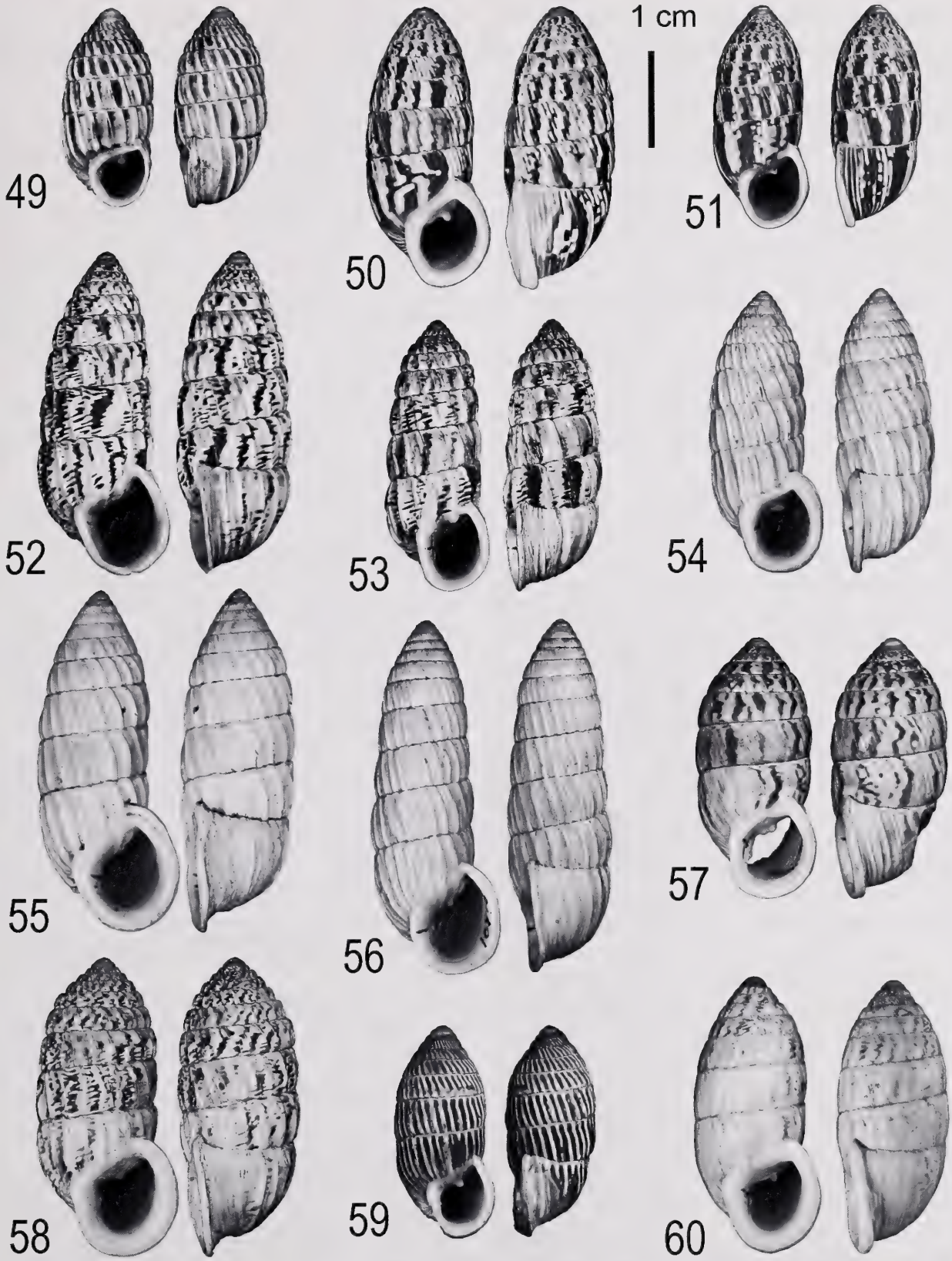
Figures 49–60. Taxon 49. *Strophia restricta* Maynard, 1894. Holotype MCZ 76384. Western end of Goat Key, Middle Bight, Andros, Bahamas. Taxon 50. *Strophia eximea* Maynard, 1894. Holotype MCZ 76243. Cat Island, Bahamas. Taxon 51. *Strophia agrestina* Maynard, 1894. Holotype MCZ 76083. South side of New Providence Island, Bahamas, opposite Nassau. Taxon 52.



Strophia scripta Maynard, 1896. Lectotype MCZ 10332. Cardenas, Cuba. Taxon 53. *Strophia scripta obliterata* Maynard, 1896. Lectotype 10335. Matanzas, Cuba, rocks close to the sea. Taxon 54. *Strophia fastigata* Maynard, 1896. Lectotype MCZ 10314. Matanzas, Cuba. Taxon 55. *Strophia eurystoma* Maynard, 1896. Lectotype MCZ 10312. Havana, Cuba. Taxon 56. *Strophia eurystoma ignota* Maynard, 1896. Lectotype MCZ 10313. Havana, Cuba. Taxon 57. *Strophia marmorata polita* Maynard, 1896. Lectotype MCZ 189792. Cabo Cruz, Cuba. Taxon 58. *Strophia media* Maynard, 1896. Lectotype MCZ 10323. Cuba. Taxon 59. *Strophia ferruginea* Maynard, 1896. Lectotype MCZ 76230. Washed up by the tide near Jeremie, southwestern Haiti. Taxon 60. *Strophia obscura* Maynard, 1896. Lectotype MCZ 76411. Cayo Birde del Norte, Cuba.

provided measurements for a single "type" specimen, the holotype, which was illustrated. Lot number MCZ 76083 contains a single specimen labeled "holotype," as well as a label with the term "Type" in Maynard's hand. It approximates the original measurements and illustration and is here recognized as the Holotype. Lot number USNM 420134 contains 200 paratypes. How many of the remaining 799 specimens are paratypes is uncertain (see Remarks).

Holotype Measurements. Length 22.8 mm, diameter (excluding lip) 9.2 mm; aperture height (including lip) 8.9 mm, aperture width (including lip and peristome) 7.2 mm.

Type Locality. South side of New Providence Island, Bahamas, opposite Nassau.

Remarks. The taxon name originally appeared as *Strophia agrestina* in the heading of the original description, but as *S. agristina* in the caption to the figure within the body of the description. The name appeared as *S. agrestina* in Maynard (1919b: 50, figs. 17, 17a, 1921b: 150, 1924c: 6) but as *S. agsestina* in Maynard (1919b, pl. 7, figs. 11–13).

Maynard (1919b: 50) acted as the First Revisor of spellings [Article 24.2.4, ICZN, 1999: 30–31], fixing the spelling as *agrestina.*

Maynard (1894b: 179) distinguished three forms [Nos. 1–3] without naming them. Specimens representing forms No. 1–3 are not paratypes of *Strophia agrestina* [Article 72.4, ICZN, 1999: 76]. Maynard (1921b: 150) noted slightly larger measurements .90 by .35 [inches; 22.9 by 8.9 mm], reported a larger number (2,000) of specimens, presumably from subsequent collections, and cited previously published illustrations (Maynard, 1919b: 52, figs. 17, pl. 7, figs. 11–13). Maynard (1924c: 6) listed *S. agrestina* as extinct in 1924 from the burning of vegetation prior to cultivation.

Taxon 52. *Strophia scripta* **Maynard, 1896 [March]: 3–4, pl. 1, figs. 3, 4.** Examined 29 specimens. Size of type 1.30 by .47 [inches; 33.0 by 11.9 mm]. Description noted, "Plate 1, fig. 3, front, fig. 4, side view of type."

Type Material. The original description provided measurements for a single "type" specimen, which was illustrated. Maynard (1896: 1) stated that he returned this figured type specimen to the MCZ but retained a co-type in his collection. Thus, these two specimens comprise the syntype series. Lot number MCZ 10332 contained two specimens labeled "holotype." The larger of the two specimens very closely approximates the originally published measurements and illustrations and is the figured specimen Maynard returned to the MCZ. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. It is unclear whether the smaller specimen [25.8 by 9.2 mm] is the syntype retained by Maynard and reacquired by the MCZ after his death or one of the 27 remaining, originally mentioned specimens, which, according to Article 72.4.6 (ICZN, 1999: 77) are expressly excluded from the type series. There are no paratypes for this taxon, and any specimens labeled as such are mislabeled. Lots MCZ 26498 (six specimens) and MCZ 76176 (five specimens) have no status as types.

Lectotype Measurements. Length 32.5 mm, diameter (excluding lip) 11.9 mm; aperture height (including lip) 11.0 mm, aperture width (including lip and peristome) 9.1 mm.

Type Locality. Cardenas, Cuba.

Remarks. Maynard (1896: 4) distinguished a single form [No. 1], composing 20% of the sample, without naming it. Maynard (1919b, pl. 7, figs. 3, 4) reillustrated this taxon.

Taxon 53. *Strophia scripta obliterata* **Maynard, 1896 [March]: 5–6, pl. 1, figs. 5, 6.** Examined 102 specimens. Size of

type 1.08 by .40 [inches; 27.4 by 10.2 mm]. Description noted, "Plate I, fig. 5, front, fig. 6, side view of type."

Type Material. The original description provided measurements for a single "type" specimen, which was illustrated. Maynard (1896: 1) stated that he returned this figured type specimen to the MCZ but retained a co-type in his collection. Thus, these two specimens compose the syntype series. Lot MCZ 10335, which was labeled "holotype," contains a single specimen accompanied by a note in Maynard's handwriting identifying the taxon and the term "type." This specimen, which closely matches the published measurements and figures, is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 100 specimens, including MCZ 26502, MCZ 26503, MCZ 26504, and MCZ 26505, are, according to Article 72.4.6 (ICZN, 1999: 77), expressly excluded from the type series. Therefore, there can be no paratypes, and any specimens labeled as such are mislabeled.

Lectotype Measurements. Length 27.5 mm, diameter (excluding lip) 10.1 mm; aperture height (including lip) 9.2 mm, aperture width (including lip and peristome) 7.3 mm.

Type Locality. Matanzas, Cuba, rocks close to the sea.

Remarks. Maynard (1896: 4) distinguished five forms [Nos. 1–5] without naming them.

Taxon 54. *Strophia fastigata* **Maynard, 1896 [March]: 6–7, pl. 2, figs. 1, 2.** Examined 62 specimens. Size of type 1.20 by .40 [inches; 30.5 by 10.2 mm]. Description noted, "Plate II, fig. 1, front, fig. 2, side view of type."

Type Material. The original description provided measurements for a single "type" specimen, which was illustrated. Maynard (1896: 1) stated that he returned this figured type specimen to the MCZ but retained a co-type in his collection. Thus, these two specimens compose the syntype series. Lot MCZ 10314 contains a single specimen labeled "Holotype," with one label annotated "id. C. J. Maynard" and another with the word "type," initialed by Maynard. Another lot, MCZ 76293, contains a single specimen and was labeled "Paratype." Although neither specimen closely matches the published measurements, the specimen in MCZ 10314 is closer and approximates the illustration of the type. This is the specimen returned to the MCZ by Maynard and is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of this taxon. The second specimen (MCZ 76293) was part of Maynard's collection at the time of his death and is the co-type that he retained. It becomes the sole paralectotype. The remaining 60 specimens (including MCZ 10314, MCZ 76293, MCZ 26513, and MCZ 26515) are, according to Article 72.4.6 (ICZN, 1999: 77), expressly excluded from the type series. Therefore, there can be no paratypes, and any specimens labeled as such are mislabeled.

Lectotype Measurements. Length 28.7 mm, diameter (excluding lip) 9.8 mm; aperture height (including lip) 10.4 mm, aperture width (including lip and peristome) 8.8 mm.

Type Locality. Maynard (1896: 7) wrote, "This species I found in the collection in the same tray with the shells which I have named *S. scripta obliterata,* therefore it is to be presumed that they came from Matanzas, Cuba, but as the shells of *S. fastigata* are deeply stained with a red earth of which those of *S. s. obliterata* bear no trace, it is evident that they did not come from "rocks close to the sea" as did the others, but probably from some neighboring field. Another lot was labeled Punte Goade, Matanzas, and still another lot Chorrea." Clench (1957: 145) listed the type locality as "Matanzas [Havana] Cuba." The lectotype is from Matanzas,

Cuba, which is the type locality (Article 76.2, ICZN, 1999: 87).

Remarks. Maynard (1896: 7) distinguished a single form [No. 1] without naming it.

Taxon 55. *Strophia eurystoma* **Maynard, 1896 [March]: 7–9, pl. 2, figs. 3, 4.** Examined 21 specimens. Size of typical specimen 1.35 by .40 [inches; 34.3 by 10.2 mm]. Description noted, "Plate II, fig. 3, front, fig. 4, side view of type."

Type Material. The original description provided measurements for a single "type" specimen, which was illustrated. Maynard (1896: 1) stated that he returned this figured type specimen to the MCZ but retained a co-type in his collection. Thus, these two specimens compose the syntype series, The remaining 19 specimens are, according to Article 72.4.6 (ICZN, 1999: 77), expressly excluded from the type series. Therefore, there can be no paratypes, and any specimens labeled as such are mislabeled. Lot MCZ 10312 contains a single specimen labeled "Holotype," with the label annotated "id. C. J. Maynard." This specimen matches closely the measurements and figures of the specimen identified as the type. It is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of this taxon.

Lectotype Measurements. Length 34.4 mm, diameter (excluding lip) 11.5 mm; aperture height (including lip) 12.6 mm, aperture width (including lip and peristome) 10.5 mm.

Type Locality. Havana, Cuba.

Remarks. Maynard (1896: 8–9) distinguished a single form [No. 1], which he provisionally named *Strophia eurystoma ignota* (see below). The taxon name also appeared as *S. eryrostoma* (Maynard, 1919c: 54).

Taxon 56. *Strophia eurystoma ignota* **Maynard, 1896 [March]: 8–9.** Not illustrated. Nine specimens [two from the MCZ, seven from another source] listed in the description of form No. 1 of *Strophia eurystoma,* but none measured.

Type Material. Maynard (1896: 1) stated that he returned figured type specimens to the MCZ and retained a co-type in his collection. Because this taxon was not figured, there is no indication that type material was designated. The original description lists a total of nine specimens, which are all syntypes. Lot MCZ 10313 contains a single specimen labeled "Holotype," with the label annotated "id. by C. J. Maynard." This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of this taxon. The remaining eight specimens, including the three specimens in MCZ 76228, become paralectotypes.

Lectotype Measurements. Length 35.9 mm, diameter (excluding lip) 10.6 mm; aperture height (including lip) 11.3 mm, aperture width (including lip and peristome) 9.3 mm.

Type Locality. Havana, Cuba.

Remarks. Maynard (1896: 8–9) distinguished a single form [No. 1] and noted that the typical form is stained by red ochraceous earth, whereas form No. 1 is stained by brown earth or without staining. On this basis, Maynard supposed that the two did not occur together. He wrote (p. 9), "Should this prove true, form No. 1 must take subspecific rank, in which case it may be called *Strophia eurystoma ignota.*"

Taxon 57. *Strophia marmorata polita* **Maynard, 1896 [March]: 14–15, pl. 3, figs. 3, 4.** Examined 25 specimens. Size of type 1.05 by .45 [inches; 26.7 by 11.4 mm]. Description noted, "Plate III, fig. 3, front, fig. 4, side view of type."

Type Material. The original description provided measurements for a single "type" specimen, which was illustrated. Maynard (1896: 1) stated that he returned this figured type specimen to the MCZ but re-

tained a co-type in his collection. Thus, these two specimens compose the syntype series. The remaining 23 specimens are, according to Article 72.4.6 (ICZN, 1999: 77), expressly excluded from the type series. Therefore, there can be no paratypes, and any specimens labeled as such are mislabeled. Lot MCZ 189792 contains a single specimen labeled "Holotype" and matches both the published measurements of the type and its illustration. This specimen has a hole in the dorsal surface of the final whorl that reveals the details of the columellar and apertural teeth. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of this taxon. A second specimen, MCZ 76201, was labeled "paratype." This specimen was part of Maynard's collection at the time of his death and is the remaining syntype, which becomes a paralectotype.

Lectotype Measurements. Length 26.1 mm, diameter (excluding lip) 11.6 mm; aperture height (including lip) 10.3 mm, aperture width (including lip and peristome) 8.9 mm.

Type Locality. Cabo Cruz, Cuba.

Remarks. Maynard (1896: 15) distinguished a single, larger form [No. 1] without naming it. Maynard (1919b, pl. 8, figs. 7, 8) reillustrated this taxon.

Taxon 58. *Strophia media* **Maynard, 1896 [March]: 18–19, pl. 4, figs. 3, 4.** Examined two specimens. Size of type 1.20 by .50 [inches; 30.5 by 12.7 mm]. Description noted, "Plate IV, fig. 3, front, fig. 4, side view of type."

Type Material. The original description provided measurements for a single "type" specimen, which was illustrated. Maynard (1896: 1) stated that he returned this figured type specimen to the MCZ but retained a co-type in his collection. Thus, the two specimens comprise the syntype series. Lot number MCZ 10323 contains a single specimen labeled "Holotype" with the label annotated "ex. C. J. Maynard." This specimen matches closely the measurements and figures of the specimen identified as the type. It is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of this taxon. Lot number MCZ 76225 contains two specimens labeled "paratype." The MCZ catalog number indicates that these specimens were among those purchased from Maynard's daughter after his death. The dead specimen is likely the remaining syntype and therefore a paralectotype. The live collected specimen might have been added after the original description and would not have any status as a type.

Lectotype Measurements. Length 30.1 mm, diameter (excluding lip) 12.2 mm; aperture height (including lip) 12.2 mm, aperture width (including lip and peristome) 10.6 mm.

Type Locality. Cuba.

Taxon 59. *Strophia ferruginea* **Maynard, 1896 [March]: 19–21, pl. 4, figs. 5, 6.** Examined nine specimens. Size of type .90 by .25 [inches; 22.9 by 6.4 mm]. Description noted, "Plate IV, fig. 5, front, fig. 6, side view of type."

Type Material. The original description provided measurements for a single "type" specimen, which was illustrated. Maynard (1896: 1) stated that he returned this figured type specimen to the MCZ but retained a co-type in his collection. Thus, the two specimens compose the syntype series. The remaining seven specimens are, according to Article 72.4.6 (ICZN, 1999: 77), expressly excluded from the type series. Therefore, there can be no paratypes, and any specimens labeled as such are mislabeled. Lot MCZ 76230 contains a single specimen labeled "Holotype" and approximates the published length (but not width, which is likely a typographical error) and illustrations of this taxon. This specimen is here designated as the lecto-

type to provide an objective standard of reference for this species-group taxon.

Lectotype Measurements. Length 21.46 mm, diameter (excluding lip) 9.25 mm; aperture height (including lip) 8.61 mm, aperture width (including lip and peristome) 6.73 mm.

Type Locality. "Washed up by the tide near Jeremie, Cote de Fer." Maynard (1896: 21) noted that "Jeremie is in Hayti, on the southwest portion," and that "Cote de Fer" refers to iron shore.

Taxon 60. *Strophia obscura* **Maynard, 1896 [March]: 21–22, pl. 3, figs. 5, 6.** Examined 50 specimens. Size of type 1.10 by .42 [inches; 27.9 by 10.7 mm]. Description noted, "Plate III, fig. 5, front, fig. 6, side view of type."

Type Material. The original description provided measurements for a single "type" specimen, which was illustrated. Maynard (1896: 1) stated that he returned this figured type specimen to the MCZ but retained a co-type in his collection. Thus, the two specimens compose the syntype series. The remaining 48 specimens are, according to Article 72.4.6 (ICZN, 1999: 77), expressly excluded from the type series. Therefore, there can be no paratypes, and any specimens labeled as such are mislabeled. Lot number MCZ 76411 contains a single specimen labeled "holotype." This specimen matches the length measurement more closely than the width measurement and approximates the figures of the specimen identified as the type. It is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of this taxon. Lots MCZ 10329 and MCZ 76410 each contain a specimen labeled "paratype." Lot number MCZ 10329 is the specimen that Maynard returned to MCZ during his lifetime. It was labeled "type" by Maynard but approximates the published measurements and figure less closely than the lectotype. This specimen came from Cayo Piedras del Norte rather than Cayo Birde del Norte. It is here considered one of the two original syntypes and becomes a paralectotype. Lot MCZ 76410 is from Cayo Birde del Norte and is likely one of the remaining 48 specimens without type status.

Lectotype Measurements. Length 27.9 mm, diameter (excluding lip) 11.1 mm; aperture height (including lip) 11.4 mm, aperture width (including lip and peristome) 9.6 mm.

Type Locality. Cayo Birde del Norte, Cuba.

Remarks. Maynard (1896: 22) distinguished a form [No. 1] composing 20% of the sample without naming it. Specimens representing this form are not paratypes of *Strophia obscura* [Article 72.4, ICZN, 1999: 76].

Taxon 61. *Strophia faxoni* **Maynard, 1896 [March]: 32–34, pl. 7, figs. 1, 2.** *S. faxsoni* Maynard, 1920a: 73. Examined two specimens. Size of type 1.12 by .40 [inches; 28.4 by 10.2 mm]. Description noted, "Plate VII, fig. 1, front, fig. 2, side view of type."

Type Material. The original description provided measurements for a single "type" specimen, which was illustrated. Maynard (1896: 1) stated that he returned this fig-

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Figures 61–73. Taxon 61. *Strophia faxoni* Maynard, 1896. Lectotype MCZ 184649. Cuba. Taxon 62. *Strophia cylindrica* Maynard, 1896. Lectotype MCZ 10311, Mathewstown, Inagua, Bahamas. Taxon 63. *Strophiops antiqua* Maynard, 1913. Lectotype MCZ 76114. Eastern Nassau, New Providence Island, Bahamas. Taxon 64. *Strophiops primigenia* Maynard, 1913. Lectotype MCZ 76088. Fossil in limestone beneath a sand cliff on the east coast of Salt Key, New Providence Island, Bahamas. Taxon 65. *Strophiops salinaria* Maynard, 1913. Lectotype MCZ 76089. Salt Key, New Providence Island, Bahamas. Taxon 66. *Strophiops larga* Maynard, 1913. Lectotype MCZ 76139. Rose Island opposite Green Key, New Providence Island, Bahamas. Taxon 67. *Strophiops affinis* Maynard, 1913. Lectotype MCZ 76091. Sandy Key, New Providence Island, Bahamas. Taxon 68. *Strophiops acceptoria* Maynard, 1913. Lectotype MCZ 76095. Low Bay Key east of Rose Island, New Providence Island, Bahamas. Taxon 69. *Strophiops cinereavaria* Maynard, 1913. Lectotype MCZ 76395. East end of Hog Island [Paradise Island], New

Providence Island, Bahamas. Taxon 70. *Strophiops variathorndikei* Maynard, 1913. Lectotype USNM 359502. Cemetery east of Nassau, New Providence Island, Bahamas. Taxon 71. *Strophiops varianivia* Maynard 1913. Lectotype MCZ 76392. About Banyan tree in Eastern Cemetery west along Shirley St. to St. Paul Quarry, Nassau, New Providence Island, Bahamas. Taxon 72. *Strophiops nivia* Maynard, 1913. [Not illustrated.] The holotype (MCZ 010279) of *Strophia curtissii nivia* Maynard, 1894 [Taxon 26], is designated as the lectotype of *Strophiops nivia* Maynard, 1913, making *Strophiops nivia* Maynard, 1913, an objective junior synonym and junior homonym of *Strophia curtissii nivia* Maynard, 1894. Taxon 73. *Strophiops rediviva* Maynard, 1913. Lectotype MCZ 76093. In field just west of St. Paul Quarry, East Nassau, New Providence Island, Bahamas.

ured type specimen to the MCZ but retained a co-type in his collection. Thus, the two specimens compose the syntype series. Clench and Aguayo (1952: 420, pl. 55, fig. 2) listed and illustrated MCZ 184649 as the "holotype." This specimen matches closely Maynard's published measurements and illustration and is accompanied by two MCZ labels. One label, with MCZ 10363 crossed out and replaced by 184649, is annotated "Type" and "id. C. J. Maynard." The other label bears the number MCZ 184649 and is annotated "ex. C. J. Maynard, Acc. 766" and labeled "Holotype." Article 74.5 (ICZN, 1999: 82–83) states, "When the original work reveals that the taxon had been based on more than one specimen, a subsequent use of the term "holotype" does not constitute a valid lectotype designation unless the author, when wrongly using that term, explicitly indicated that he or she was selecting from the type series that particular specimen to serve as the name-bearing type." Thus, there is no holotype for this taxon, nor can Clench and Aguayo's treatment of MCZ 184649 be considered a lectotype designation. This specimen [MCZ 184649] is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original and Clench and Aguayo's subsequent concepts of this taxon.

Lectotype Measurements. Length 28.9 mm, diameter (excluding lip) 10.2 mm; aperture height (including lip) 9.6 mm, aperture width (including lip and peristome) 8.5 mm.

Type Locality. Cuba.

Remarks. Maynard (1896: 34) commented that "Although these specimens were simply labeled 'Cuba,' I have no doubt but what they came from the neighborhood of Gibara, Cuba."

Taxon 62. *Strophia cylindrica* **Maynard, 1896 [March]: 34–36, pl. 7, figs. 3, 4.** Number of specimens examined not specified. Size of type 1.10 by .40 [inches; 27.9 by 10.2 mm]. Description noted, "Plate VII, fig. 3, front, fig. 4, side view of type."

Type Material. The original description provided measurements for a single "type" specimen, which was illustrated. Maynard (1896: 1) stated that he returned this figured type specimen to the MCZ but retained a co-type in his collection. Thus, these two specimens compose the syntype series. Of these, MCZ 10311, which was labeled "Holotype" and contains a single specimen accompanied by a note in Maynard's handwriting identifying the taxon but not using the term "type," is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The unspecified number of additional specimens are, according to Article 72.4.6 (ICZN, 1999: 77), expressly excluded from the type series. Therefore, there can be but one paralectotype.

Lectotype Measurements. Length 27.2 mm, diameter (excluding lip) 9.8 mm; aperture height (including lip) 9.0 mm, aperture width (including lip and peristome) 7.7 mm.

Type Locality. Mathewstown, Inagua [Bahamas], from town border to salina.

Remarks. Maynard (1896: 35) distinguished four forms [Nos. 1–4] without naming them. Maynard (1919b, fig. 13, pl. 7, figs. 1, 2) reillustrated this taxon. Clench (1959: 45) listed this taxon as a synonym of *Cerion* (*Diacerion*) *rubicundum* (Menke, 1829) but did not select a lectotype.

Taxon 63. *Strophiops antiqua* **Maynard, 1913b [February 1]: 183–184** [not illustrated in original publication]. Examined 375 specimens. Size given as 1.25 by .50 [inches; 31.8 by 12.7 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 375 specimens examined, and there was no mention of type material in the other parts of this

publication. Thus, all 375 specimens are syntypes. Lot number MCZ 76114 contains a single specimen labeled "holotype." Although the width of this specimen matches the published measurement, the length differs by nearly 10%. The specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 374 specimens, including MCZ 76115 and MCZ 117863, become paralectotypes.

Lectotype Measurements. Length 29.0 mm, diameter (excluding lip) 12.7 mm; aperture height (including lip) 11.1 mm, aperture width (including lip and peristome) 9.9 mm.

Type Locality. Eastern Nassau [New Providence Island, Bahamas]. Fossil. Maynard's handwritten note accompanying the type specimen states "crab holes, Waterloo."

Remarks. Maynard (1913b: 183–184) surmised that, "Neither this nor the above [*S. agassizii*] appear to be ancestors of any living form thus discovered." Maynard (1921b: 151) reported 400 specimens and provided citations to illustrations (pl. 47, figs. 3, 4) that were never issued. Gould and Woodruff (1986: 480) reported examining the "holotype" and provisionally considered this taxon to be a synonym of *Cerion agassizii* Dall, 1894.

Taxon 64. *Strophiops primigenia* **Maynard, 1913b [February 1]: 184** [not illustrated in original publication]. Examined 100 specimens. Size given as 1.50 by .50 [inches; 38.1 by 12.7 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 100 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 100 specimens are syntypes. Lot number MCZ 76088 contained 56 specimens and was labeled "paratype." This lot also contained labels in Maynard's hand identifying the specimens as "typical," but none use the word "type" nor refer to the subsequently published illustrations. A large specimen that approximates the published measurements and subsequently published illustration is selected as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of it. The remaining 55 specimens were recatalogued as MCZ 356992 and are paralectotypes.

Lectotype Measurements. Length 35.0 mm, diameter (excluding lip) 12.4 mm; aperture height (including lip) 11.2 mm, aperture width (including lip and peristome) 9.7 mm.

Type Locality. Fossil in limestone beneath a sand cliff on the east coast of Salt Key, New Providence Island, Bahamas.

Remarks. Maynard (1913b: 184) considered this to be the ancestor of all the species in the "Primigenia Group" [an "aggregate of species" sensu Article 10.4 (ICZN, 1999: 9) rather than a genus-group taxon]. *Strophiops primigenia* was subsequently illustrated (Maynard, 1924a, pl. 39, figs. 3, 4). Maynard (1921b: 142) provided slightly smaller measurements and a different locality (east of Rose Island). Gould and Woodruff (1986: 481) doubted that this taxon was truly a fossil, and regarded it to be a synonym of *Cerion glans* (Küster, 1844).

Taxon 65. *Strophiops salinaria* **Maynard, 1913b [February 1]: 184** [not illustrated in original publication]. Examined 500 specimens. Size given as 1.35 by .45 [inches; 34.3 by 11.4 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 500 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 500 specimens are syntypes. Lot number MCZ 76089 contains a single specimen that was catalogued as the "Holotype" and that was il-

lustrated by Gould and Woodruff (1978, fig. 2) and captioned "holotype." Gould and Woodruff's caption cannot be accepted as a lectotype designation, as Article 74.5 (ICZN, 1999: 83) states, "When the original work reveals that the taxon had been based on more than one specimen, a subsequent use of the term 'holotype' does not constitute a valid lectotype designation unless the author, when wrongly using that term, explicitly indicated that he or she was selecting from the type series that particular specimen to serve as the name-bearing type." This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 499 specimens, including MCZ 76090 and USNM 420055 (15 specimens), become paralectotypes.

Lectotype Measurements. Length 30.5 mm, diameter (excluding lip) 11.9 mm; aperture height (including lip) 10.2 mm, aperture width (including lip and peristome) 8.4 mm.

Type Locality. Living all over Salt Key [New Providence Island, Bahamas], and thousands dead in the sand cliff at the east end.

Remarks. Maynard (1921b: 144, 1925, pl. 40, figs. 1, 2) published larger dimensions of 1.45 by .45 [inches; 36.8 by 11.4 mm] and illustrations of this taxon. Gould and Woodruff (1986: 475) regarded this taxon to be a synonym of *Cerion glans* (Küster, 1844).

Taxon 66. *Strophiops larga* **Maynard, 1913b [February 1]: 184**; Maynard, 1921b: 145; Maynard, 1925, pl. 41, figs. 3, 4. Examined 20 specimens [not illustrated in original publication]. No measurements included in original description.

Type Material. The original description did not distinguish among the 20 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 20 specimens are syntypes. Lot number MCZ 76139 contains a single specimen labeled "holotype." This lot also contains a label in Maynard's hand with the term "type," which includes references to illustrations (Maynard, 1925, pl. 41, figs. 3, 4) that were published 12 years after the species was described. This specimen approximates the subsequently published measurements and is the specimen figured in 1925 [a repaired break on the apertural surface is present in both figure and specimen]. It is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of this taxon. The remaining 19 syntypes, including MCZ 76140, become paralectotypes.

Lectotype Measurements. Length 32.1 mm, diameter (excluding lip) 12.8 mm; aperture height (including lip) 12.0 mm, aperture width (including lip and peristome) 10.4 mm.

Type Locality. Rose Island opposite Green Key [New Providence Island, Bahamas].

Remarks. Maynard (1921b: 145) provided measurements 1.35 by .52 [inches; 34.3 by 13.2 mm] and references to subsequently published illustrations but listed a slightly different locality, "West shore of Hog Island opposite Green Key," and noted 25 specimens, some perhaps subsequently collected. Gould and Woodruff (1986: 475) regarded this taxon to be a synonym of *Cerion glans* (Küster, 1844).

Taxon 67. *Strophiops affinis* **Maynard, 1913b [February 1]: 184–185** [not illustrated in original publication]. Examined 300 specimens. Size given as 1.15 by 60 [sic .60] [inches; 29.2 by 15.2 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 300 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 300 specimens are

syntypes. Lot number MCZ 76091 contains a single specimen labeled "holotype." This lot also contains a label in Maynard's hand with the term "Type" that includes references to illustrations (pl. 44, figs. 7, 8), which were never published. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of this taxon. The remaining 229 syntypes, including MCZ 76092, become paralectotypes.

Lectotype Measurements. Length 30.9 mm, diameter (excluding lip) 12.3 mm; aperture height (including lip) 11.4 mm, aperture width (including lip and peristome) 9.4 mm.

Type Locality. The original description listed this taxon as occurring on Sandy and Green Keys [New Providence Island, Bahamas], living under different environments on each. Because the lectotype is from Sandy Key, the type locality is restricted to Sandy Key (Article 76.2, ICZN, 1999: 87).

Remarks. Maynard (1921b: 144) provided slightly different measurements [1.20 by .57 inches; 30.5 by 14.4 mm] and a reference to figures [pl. 44, figs. 5, 6; these figure numbers differ from those on the label accompanying the lectotype] that were never published. Gould and Woodruff (1986: 474) had examined the "Holotype" and synonymized this taxon with *Cerion glans* (Küster, 1844).

Taxon 68. *Strophiops acceptoria* **Maynard, 1913b [February 1]: 185** [not illustrated in original publication]. Examined 200 specimens. Size given as .94 by .36 [inches; 23.9 by 9.1 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 200 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 200 specimens are syntypes. Lot number MCZ 76095 was labeled "Holotype," but contained two specimens. One of the specimens approximates the measurements and subsequent figure [Maynard, 1925, pl. 41, figs. 5, 6] and is here selected as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of this taxon. The remaining 199 syntypes became co-mingled with additional specimens (see Remarks), so it is unclear which of the specimens in MCZ 76096 (223 specimens) and USNM 420075 (110 specimens), are paralectotypes.

Lectotype Measurements. Length 25.4 mm, diameter (excluding lip) 10.6 mm; aperture height (including lip) 9.4 mm, aperture width (including lip and peristome) 7.8 mm.

Type Locality. Low Bay Key east of Rose Island [New Providence Island, Bahamas].

Remarks. Maynard (1921b: 145) noted a larger size (1.00 by .40 [inches]), a larger number (528) of specimens, likely the result of subsequent collections, and provided references to figures (pl. 41, figs. 5, 6) that were issued in 1925. Gould and Woodruff (1986: 474) had examined the "Holotype" and synonymized this taxon with *Cerion glans* (Küster, 1844).

Taxon 69. *Strophiops cinereavaria* **Maynard, 1913b [February 1]: 185** [not illustrated in original publication]. Examined 614 specimens. No measurements included in description.

Type Material. The original description did not distinguish among the 614 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 614 specimens are syntypes. Lot number MCZ 76395 contained five specimens labeled "paratype." Examination of the MCZ catalog revealed that no single specimen identified as a type was present in Maynard's collection when it was acquired from his daughter. Because neither measurements nor illustrations were ever published for this taxon, one of

the five specimens, the best preserved undamaged adult, is selected to be the lectotype to provide an objective standard of reference for this species-group taxon. The remaining specimens, recatalogued as MCZ 356476, become paralectotypes.

Lectotype Measurements. Length 29.1 mm, diameter (excluding lip) 11.9 mm; aperture height (including lip) 11.0 mm, aperture width (including lip and peristome) 9.9 mm.

Type Locality. East end of Hog Island [Paradise Island] [New Providence Island, Bahamas].

Remarks. The taxon name originally appeared as *S. cinerea-vara,* but was used as *S. cinerea-varia* on the following page. A correction was published (Maynard, 1913c: 199) in which Maynard acted as the First Revisor of spellings [Article 24.2.4, ICZN, 1999: 30–31], selecting *cineria-varia* to be the correct spelling. Following Article 32.5.2.4 (ICZN, 1999: 40), the hyphen is removed and the taxon becomes *cinereavaria.* Gould and Woodruff (1986: 474) reported examining "paratypes" and synonymized this taxon with *Cerion glans* (Küster, 1844).

Taxon 70. *Strophiops variathorndikei* **Maynard, 1913b [February 1]: 186** [not illustrated in original publication]. Number of specimens examined not specified. No measurements included in description.

Type Material. The original description did not specify the number of specimens examined, which are all syntypes. This taxon was not represented in the collections of MCZ, nor was it present in Maynard's collection at the time it was acquired from his daughter, as revealed by an examination of the MCZ catalog. The USNM catalog revealed that USNM 359502 contained four syntypes that Bartsch had purchased from Maynard. Because neither measurements nor illustration were published, one of the specimens in this lot, a well-preserved undamaged adult, is selected to serve as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining three specimens, recatalogued as USNM 1093789, become paralectotypes.

Lectotype Measurements. Length 19.1 mm, diameter (excluding lip) 8.4 mm; aperture height (including lip) 7.4 mm, aperture width (including lip and peristome) 6.4 mm.

Type Locality. Cemetery east of Nassau [New Providence Island, Bahamas].

Remarks. Following Article 32.5.2.4 (ICZN, 1999: 40) the hyphen is removed from *varia-thorndikei* and the taxon becomes *variathorndikei.* A label accompanying the lectotype stated, "on an isolated grass plot, now extinct. 1915." Gould and Woodruff (1986: 478) regarded this taxon to be a synonym of *Cerion gubernatorium* (Crosse, 1869).

Taxon 71. *Strophiops varianivia* **Maynard 1913b [February 1]: 186** [not illustrated in original publication]. Number of specimens examined not specified. No measurements included in description.

Type Material. The original description did not specify the number of specimens examined, which are all syntypes. No specimen labeled holotype could be found at the MCZ. Lot MCZ 76392 contained 22 mostly juvenile specimens labeled "paratypes." One of the adult specimens in this lot is selected as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 21 specimens, recatalogued as MCZ 356675, become paralectotypes.

Lectotype Measurements. Length 19.6 mm, diameter (excluding lip) 9.0 mm; aperture height (including lip) 8.0 mm, aperture width (including lip and peristome) 6.6 mm.

Type Locality. About Banyan tree in Eastern Cemetery west along Shirley St.

to St. Paul Quarry [Nassau, New Providence Island, Bahamas].

Remarks. The first use of this name was in the form of a citation, as if it were previously published. See remarks under *Strophia curtissii nivia* [Taxon 26]. Following Article 32.5.2.4 (ICZN, 1999: 40) the hyphen is removed from *varia-nivia* and the taxon becomes *varianivia.* Gould and Woodruff (1986: 478) regarded this taxon to be a synonym of *Cerion gubernatorium* (Crosse, 1869).

Taxon 72. *Strophiops nivia* **Maynard, 1913b [February 1]: 186** [not illustrated in original publication]. Examined 829 specimens. No measurements included in description. See remarks under *Strophia curtissii nivia* Maynard, 1894 [Taxon 26].

Nomenclatural Remarks. This taxon was described as new, appearing as "*S. nivia* new," whereas the preceding taxon, *S. varia-nivia,* was incorrectly listed as being previously described, appearing as "*S. varia-nivia* Mayn." This is almost certainly an error in typesetting. *Strophiops nivia* Maynard, 1913, is a junior homonym of *Strophia curtissii nivia* Maynard, 1894.

Type Material. The number of specimens listed in Maynard (1913b: 186, 1919b: 47) was substantially higher than the 40 listed in the original description of *S. curtissii nivia* (Maynard, 1894: 112). It is likely that Maynard added specimens in subsequent field work. The type localities for both uses of the name are identical except for phrasing, and only one series of specimens bearing the name *nivia* was present in Maynard's collection at the time it was acquired from his daughter. The holotype of *Strophia curtissii nivia* Maynard, 1894 (MCZ 10279), is here designated as the lectotype of *Strophiops nivia* Maynard, 1913, making *Strophiops nivia* Maynard, 1913, both a junior secondary homonym and an objective junior synonym of *Strophia curtissii nivia* Maynard, 1894.

Remarks. Clench (1957: 155) listed *S. nivia* as an error for *S. nivea* Maynard, 1894, rather than as a separately described taxon.

Taxon 73. *Strophiops rediviva* **Maynard, 1913c [February 9]: 187**; Maynard, 1921b: 144; Maynard, 1925, pl. 40, figs. 5, 6 [not illustrated in original publication]. Examined 500 specimens. No measurements included in description.

Type Material. The original description did not distinguish among the 500 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 500 specimens are syntypes. Lot MCZ 76093 was labeled "Holotype" but contained two specimens and a label written by Maynard that contains the name of the taxon, the word "type," and "Plate 40 figs. 5 6." The specimen that closely resembles the published illustration is here selected as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of this taxon. The other specimen, recatalogued as MCZ 356478, and MCZ 76094 are among the 499 paralectotypes.

Lectotype Measurements. Length 29.8 mm, diameter (excluding lip) 11.1 mm; aperture height (including lip) 10.5 mm, aperture width (including lip and peristome) 8.3 mm.

Type Locality. In field just west of St. Paul Quarry, East Nassau [New Providence Island, Bahamas].

Remarks. Maynard (1921b: 144) noted that the taxon was collected in 1897 but was extinct in 1921. Maynard (1924c: 6) listed *S. rediviva* as extinct in 1913 from the burning of vegetation prior to cultivation. Maynard (1925, pl. 40, figs. 5, 6) provided colored illustrations for this taxon. Gould and Woodruff (1986: 476) regarded this taxon to be "intermediate" between *Cerion glans* (Küster, 1844) and *C. gubernatorium* (Crosse, 1869).

Taxon 74. *Strophiops variapurpurea* **Maynard, 1913c [February 9]: 188** [not

illustrated in original publication]. Examined 59 specimens. No measurements included in description.

Type Material. The original description did not distinguish among the 59 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 59 specimens are syntypes. No specimen labeled "Holotype" could be found at the MCZ. Lot MCZ 76286 contained 15 specimens labeled "paratypes." One of these specimens, a well-preserved undamaged adult, was selected as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 58 specimens, including the 14 specimens recatalogued as MCZ 356676, become paralectotypes.

Lectotype Measurements. Length 23.4 mm, diameter (excluding lip) 10.1 mm; aperture height (including lip) 8.9 mm, aperture width (including lip and peristome) 7.5 mm.

Type Locality. From the termination of Bay Street east to the Creek Settlement [Nassau, New Providence Island, Bahamas].

Remarks. Following Article 32.5.2.4 (ICZN, 1999: 40), the hyphen is removed from *varia-purpurea* and the taxon becomes *variapurpurea.* Gould and Woodruff (1986: 478) regarded this taxon to be a synonym of *Cerion gubernatorium* (Crosse, 1869).

Taxon 75. *Strophiops purpurea* **Maynard, 1913c [February 9]: 188–189**; Maynard, 1921b: 150 [not illustrated in original publication]. Examined 50 specimens. Size given as 1.05 by .40 [inches; 26.7 by 10.2 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 50 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 50 specimens are syntypes. Lot MCZ 76108 contains a single specimen labeled "Holotype." This lot also contains a label in Maynard's hand with the term "type" that includes references to illustrations (pl. 46, figs. 2, 3) that were never published. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of this taxon. The remaining 49 syntypes become paralectotypes. Lot MCZ 76107 contains 92 specimens, indicating that at least 43 were collected after the taxon was described.

Lectotype Measurements. Length 26.1 mm, diameter (excluding lip) 10.3 mm; aperture height (including lip) 10.1 mm, aperture width (including lip and peristome) 8.4 mm.

Type Locality. Creek Settlement, east about 1 mile along the shore [Nassau, New Providence Island, Bahamas].

Remarks. Maynard (1919a: 24) misspelled the name as *S. purpura.* Maynard

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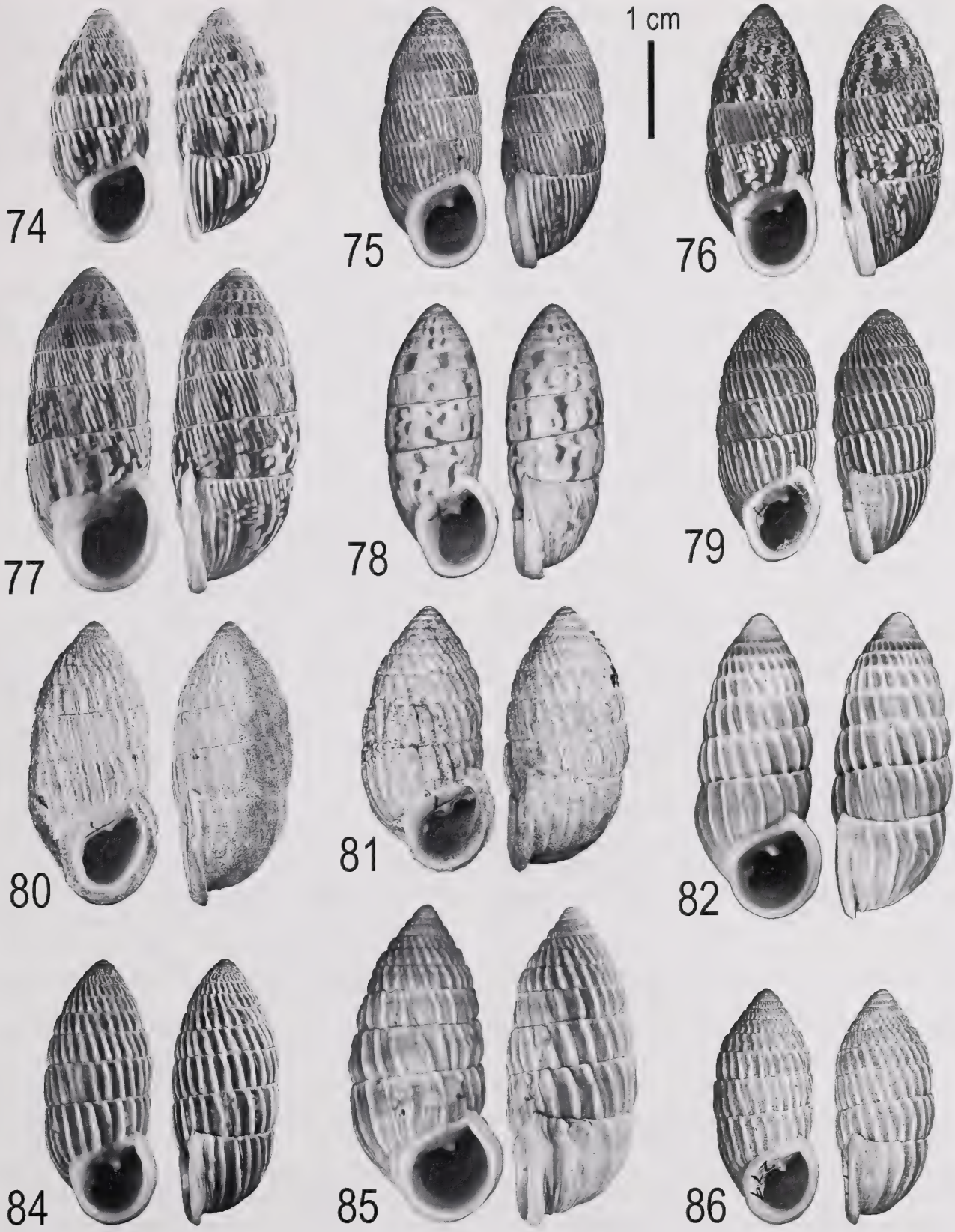
Figures 74–86. Taxon 74. *Strophiops variapurpurea* Maynard, 1913. Lectotype 76286. Found from the termination of Bay Street east to the Creek Settlement, Nassau, New Providence Island, Bahamas. Taxon 75. *Strophiops purpurea* Maynard, 1913. Lectotype MCZ 76108. Creek Settlement, east about 1 mile along the shore, Nassau, New Providence Island, Bahamas. Taxon 76. *Strophiops macularia* Maynard, 1913. Lectotype 76127. South shore New Providence Island, Bahamas, from west side of first sound west 2 miles to a salina and northward along an old disused road running from the beach to Fox Hill, 1 mile. Taxon 77. *Strophiops rufimaculata* Maynard, 1913. Lectotype MCZ 76126. South shore of New Providence Island, Bahamas, from west side of salina to Sound Point, 2 miles. Taxon 78. *Strophiops delicata* Maynard, 1913. Lectotype MCZ 76099. South Key off Sound Point, New Providence Island, Bahamas. Taxon 79. *Strophiops ultima* Maynard, 1913. Lectotype 76154. Southwest Key, New Providence Island, Bahamas. Taxon 80. *Strophiops avita* Maynard, 1913. Lectotype MCZ 76394. Silver Key just west of Nassau Bar, New Providence Island, Bahamas, under a bed of limestone a foot thick, embedded in an ancient red soil. Taxon 81. *Strophiops vetusta* Maynard, 1913. Lectotype MCZ 117930. Fossil in the limestone of the three Silver Keys off Nassau Bar and of the Pimlico Keys off Eleuthera, Bahamas. Taxon 82. *Strophiops argentia* Maynard, 1913. Lectotype MCZ 76120. Living



on the three Silver Keys, Nassau, New Providence Island, Bahamas. Taxon 83. *Strophiops agavaneglecta* Maynard, 1913. [Not illustrated.] The holotype (MCZ 76103) of *Strophia neglecta agava* Maynard, 1894 [Taxon 41], is designated as the neotype of *Strophiops agavaneglecta* Maynard, 1913, making *Strophiops agavaneglecta* Maynard, 1913, an objective junior synonym of *Strophia neglecta agava* Maynard, 1894. Taxon 84. *Strophiops oberholseri* Maynard, 1913. Lectotype MCZ 76124. Southwest Bay, New Providence Island, Bahamas. Taxon 85. *Strophiops inconsueta* Maynard, 1913. Lectotype MCZ 76123. Southern portion of Great Pimlico Island, Eleuthera, Bahamas. Taxon 86. *Strophiops transitoria* Maynard, 1913. Lectotype MCZ 117848. Northern portion of Great Pimlico Island, Eleuthera, Bahamas.

(1921b: 150) reported 705 mostly dead specimens collected from the back of a sandy beach, just southwest of East Point Light on New Providence Island and cited illustrations (pl. 46, figs. 2, 3) that were never issued. Maynard (1924?) listed this taxon as *S. purpurea* in the catalog, but in the supplement to the catalog (1924c: 6) reported *S. "purpura"* as extinct in 1924 from the burning of vegetation prior to cultivation. Gould and Woodruff (1986: 478) regarded this taxon to be a synonym of *Cerion gubernatorium* (Crosse, 1869).

Taxon 76. *Strophiops macularia* **Maynard, 1913c [February 9]: 189**; Maynard, 1921b: 150 [not illustrated in original publication]. Examined 325 specimens. Size given as 1.18 by .45 [inches; 30.0 by 11.4 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 325 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 325 specimens are syntypes. Lot MCZ 76127 contains a single specimen labeled "holotype." This lot also contains a label in Maynard's hand with the term "type," which includes references to illustrations (pl. 46, figs. 4, 5) that were never published. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of this taxon. The remaining 324 syntypes, including MCZ 76128, become paralectotypes.

Lectotype Measurements. Length 27.4 mm, diameter (excluding lip) 11.0 mm; aperture height (including lip) 10.5 mm, aperture width (including lip and peristome) 8.4 mm.

Type Locality. South shore New Providence [Island, Bahamas] from west side of first sound west 2 miles to a salina and northward along an old disused road running from the beach to Fox Hill, 1 mile.

Remarks. Maynard (1921b: 150) provided slightly smaller measurements (1.10 by .45 [inches; 27.9 by 11.4 mm]) and reported a larger number (2,041) of specimens, presumably from subsequent collections. The illustrations cited (pl. 46, figs. 5, 6) were never issued. Gould and Woodruff (1986: 478) regarded this taxon to be a synonym of *Cerion gubernatorium* (Crosse, 1869).

Taxon 77. *Strophiops rufimaculata* **Maynard, 1913c [February 9]: 189–190**; Maynard, 1921b: 150 [not illustrated in original publication]. Examined 325 specimens. Size given as 1.25 by .50 [inches; 32.8 by 12.7 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 325 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 325 specimens are syntypes. No specimen labeled "Holotype" could be found at the MCZ. Lot MCZ 76126 contained 136 specimens labeled "Paratypes." Because this taxon was never illustrated, one of the syntypes that most closely approximates the published dimensions was selected as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 135 specimens were recatalogued as MCZ 356474 and are among the remaining 324 syntypes that become paralectotypes.

Lectotype Measurements. Length 32.2 mm, diameter (excluding lip) 12.6 mm; aperture height (including lip) 12.6 mm, aperture width (including lip and peristome) 11.1 mm.

Type Locality. South shore of New Providence [Island, Bahamas] from west side of salina to Sound Point, 2 miles.

Remarks. Maynard (1921b: 150) cited illustrations (pl. 46, figs. 7, 8) that were never issued. Gould and Woodruff (1986: 478) regarded this taxon to be a synonym of *Cerion gubernatorium* (Crosse, 1869).

Taxon 78. *Strophiops delicata* **Maynard, 1913c [February 9]: 190**; Maynard, 1921b: 151 [not illustrated in original publication]. Examined 107 specimens. Size given as 1.10 by .35 [inches; 27.9 by 8.9 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 107 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 107 specimens are syntypes. Lot MCZ 76099 was labeled "holotype" but contains two specimens accompanied by a note in Maynard's handwriting identifying the taxon and containing the term "types (2)," as well as the notation "Plate 46 figs. 9–10." Both specimens are nearly identical in measurements. One specimen (MCZ 76099) is here selected as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The other specimen was recatalogued as MCZ 356477 and is among the remaining 106 syntypes, including MCZ 76100, which become paralectotypes.

Lectotype Measurements. Length 27.6 mm, diameter (excluding lip) 9.8 mm; aperture height (including lip) 10.3 mm, aperture width (including lip and peristome) 8.5 mm.

Type Locality. South Key off Sound Point [New Providence Island, Bahamas].

Remarks. Maynard (1921b: 150) cited illustrations (pl. 46, figs. 9, 10) that were never issued. Gould and Woodruff (1986: 478) regarded this taxon to be a synonym of *Cerion gubernatorium* (Crosse, 1869).

Taxon 79. *Strophiops ultima* **Maynard, 1913c [February 9]: 190**; Maynard, 1921b: 151 [not illustrated]. Number of specimens examined not specified [Maynard, 1921b: 151, mentioned 200 specimens]. Size given as .95 by .40 [inches; 24.1 by 10.2 mm], but the term "type" was not used.

Type Material. The original description did not specify the number of specimens examined, which are all syntypes. Lot MCZ 76154 was labeled "Holotype" and contains a single specimen accompanied by a note in Maynard's handwriting identifying the taxon and containing the term "type" as well as the notation "Plate 45 figs. 1–2." The illustrations were never published, nor were illustrations mentioned in the subsequent treatment of the taxon (Maynard, 1921b: 151). This specimen (MCZ 76154) approximates the published measurements and is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. It is not clear how many of the subsequently mentioned 200 specimens were available to Maynard at the time he described this taxon. Lot MCZ 76153 contains 523 specimens, most of which could not have been part of the type series.

Lectotype Measurements. Length 25.1 mm, diameter (excluding lip) 10.2 mm; aperture height (including lip) 9.8 mm, aperture width (including lip and peristome) 8.1 mm.

Type Locality. No locality was mentioned in the original publication. Maynard (1921b: 151) reported the locality as Southwest Key, New Providence Island, Bahamas. This is also the data accompanying the lectotype.

Remarks. Maynard commented that this is "another fine example of recession with four species intervening between it and the species it mimics, two of them white!" Gould and Woodruff (1986: 474) had examined "paratypes" and synonymized this taxon with *Cerion glans* (Küster, 1844).

Taxon 80. *Strophiops avita* **Maynard, 1913c [February 9]: 190** [not illustrated in original publication]; Maynard, 1914a: front cover; Maynard, 1914b: front cover; Maynard, 1921a: 138; Maynard, 1921b, pl. 35, figs. 1, 2. Examined 50 specimens. Size given as 1.10 by .45

[inches; 27.9 by 11.4 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 50 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 50 specimens are syntypes. Lot MCZ 76394 was labeled "Holotype" and contains a single specimen accompanied by a note in Maynard's handwriting identifying the taxon and containing the term "type." It is within 7% of the measurements included in the original description and approximates the subsequent illustration of this species on the front covers of Maynard (1914a,b), more so than the later illustration (Maynard, 1921b, pl. 35, figs. 1, 2), which has a more conical spire. This specimen (MCZ 76394) is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The original description states that 50 specimens were examined; thus, the remaining 49, including MCZ 76141, become paralectotypes. However, Maynard, 1921a (p. 138), lists 55 specimens, some possibly subsequently collected.

Lectotype Measurements. Length 28.6 mm, diameter (excluding lip) 12.2 mm; aperture height (including lip) 12.2 mm, aperture width (including lip and peristome) 10.1 mm.

Type Locality. Silver Key just west of Nassau Bar [New Providence Island, Bahamas]. Found under a bed of limestone a foot thick embedded in an ancient red soil.

Remarks. Maynard (1913c: 190) opined that this was "undoubtedly the oldest fossil *Strophia* yet found in the Bahamas." Gould and Woodruff (1986: 474) synonymized this taxon with *Cerion agassizii* Dall, 1894, but noted that the "Holotype" resembled *C. glans* (Küster, 1844).

Taxon 81. *Strophiops vetusta* **Maynard, 1913c [February 9]: 191** [not illustrated in original publication]; Maynard, 1921a: 138; Maynard, 1921b, pl. 35, figs. 3, 4. Examined 200 specimens. Size given as 1.25 by .50 [inches; 31.8 by 12.7 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 200 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 200 specimens are syntypes. Lot MCZ 117930 was labeled "co-type" and contains a single specimen accompanied by a note in Maynard's handwriting dated "10/9/14," identifying the taxon and containing the term "co-type." This specimen is significantly (14%) shorter than the measurements included in the original description but approximates the subsequent illustration of this species (Maynard, 1921b, pl. 35, figs. 3, 4). This specimen (MCZ 117930) is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 199 syntypes, including MCZ 76129, become paralectotypes. Maynard (1921a: 138) listed 265 specimens, some possibly subsequently collected.

Lectotype Measurements. Length 26.8 mm, diameter (excluding lip) 12.2 mm; aperture height (including lip) 11.2 mm, aperture width (including lip and peristome) 9.6 mm.

Type Locality. Fossil in the limestone of the three Silver Keys off Nassau Bar [New Providence Island], and of the Pimlico Keys off Eleuthera [Bahamas]. The label accompanying the lectotype states Silver Key, thus restricting the type locality.

Remarks. Clench (1952: 110) listed this taxon as a junior synonym of *Cerion inconsuetum* (Maynard, 1913). Gould and Woodruff (1986: 482) listed this taxon as a synonym of *C. glans* (Küster, 1844).

Taxon 82. *Strophiops argentia* **Maynard, 1913c [February 9]: 191** [not illustrated in original publication]. *S. ar-*

gntea Maynard, 1921a: 138; Maynard, 1921b: 139, pl. 35, figs. 5, 6 [*S. argentea* in plate caption]. Examined 400 specimens. Size given as 1.20 by .45 [inches; 30.5 by 11.43 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 400 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, there is no holotype for this taxon, and the species is based on 400 syntypes. Lot MCZ 76120 was labeled "Holotype" and contained a single specimen accompanied by a note in Maynard's handwriting that identified the taxon and contained a reference to subsequently published illustrations (Maynard, 1921b, pl. 35, figs. 5, 6) but did not include any form of the word "type." This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 399 syntypes (including MCZ 76121, MCZ 118064, and USNM 419999) become paralectotypes.

Lectotype Measurements. Length 30.1 mm, diameter (excluding lip) 11.5 mm; aperture height (including lip) 10.3 mm, aperture width (including lip and peristome) 9.5 mm.

Type Locality. Living on the three Silver Keys [New Providence Island, Bahamas].

Remarks. Maynard (1913c: 150) noted "Silver Key, the most western of the group, is remarkable as having been the home of three, quite closely allied and evidently successive species of Strophias, representatives of the three distinct geological periods." This taxon name was misspelled as *S. argntea in* Maynard, 1921a (p. 138), and as *S. argentea* in captions (Maynard, 1919c, fig. 26, 1921b, pl. 35, figs. 5, 6) and the sales catalog (Maynard, 1924?: [4]). Gould and Woodruff (1986: 474) listed this taxon as a synonym of *Cerion glans* (Küster, 1844).

Taxon 83. *Strophiops agavaneglecta* **Maynard, 1913c [February 9]: 192** [not illustrated]. Examined 150 specimens. No measurements provided.

Type Material. The original description did not distinguish among the 150 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 150 specimens are syntypes. This taxon was not represented in the collections of MCZ, nor was it present in Maynard's collection at the time it was acquired from his daughter, as revealed by an examination of the MCZ catalog. This taxon was not among the material purchased for the USNM collections either during Maynard's lifetime or from his estate. Searches of the collections and/or databases of The Academy of Natural Sciences of Philadelphia, The Field Museum of Natural History, The Florida Museum of Natural History, and The Museum of Biological Diversity, The Ohio State University, failed to uncover a single specimen catalogued under this name. This taxon was never illustrated, nor did it appear in any of Maynard's subsequent publications or catalogs. The description is limited to the statement "Intermediate between *agava* and *neglecta.*" [*Strophia agava* was originally proposed as a subspecies of *S. neglecta*.] No specimens bearing the name *Strophiops agavaneglecta* could be located in museums, nor could this taxon be identified on the basis of its limited description. The holotype of *Strophia neglecta agava* Maynard, 1894 (MCZ 76103), is here designated as the neotype of *Strophiops agavaneglecta* Maynard, 1913, to provide an objective standard of reference for this species-group taxon. *Strophiops agavaneglecta* Maynard, 1913, becomes an objective junior synonym of *Strophia neglecta agava* Maynard, 1894.

Type Locality. Maynard (1913c: 192) defined the type locality of *S. agavaneglecta* to be the eastern portion of the range of *S. agava* [fields west of Nassau, New Providence Island, Bahamas]. With

the neotype designation, the type locality of *S. agava* becomes the type locality of *S. agavaneglecta* (Article 76.3, ICZN, 1999: 87).

Remarks. Following Article 32.5.2.4 (ICZN, 1999: 40), the hyphen is removed from *agava-neglecta* and the taxon becomes *agavaneglecta.* Gould and Woodruff (1986: 474) synonymized this taxon with *Cerion glans* (Küster, 1844).

Taxon 84. *Strophiops oberholseri* **Maynard, 1913c [February 9]: 193** [not illustrated in original publication]; Maynard, 1920c, fig. 86; Maynard, 1921b: 140, pl. 37, figs. 1, 2. Examined 220 specimens. No measurements provided in original description.

Type Material. The original description did not distinguish among the 220 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 220 specimens are syntypes. Lot MCZ 76124 contains a single specimen labeled "holotype." This lot also contains a label in Maynard's hand with the term "Type" that includes references to subsequently published illustrations (Maynard, 1921b, pl. 37, figs. 1, 2), which the specimen approximates. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of this taxon. The remaining 219 syntypes, including MCZ 76125 and MCZ 117655, become paralectotypes.

Lectotype Measurements. Length 26.4 mm, diameter (excluding lip) 10.6 mm; aperture height (including lip) 9.7 mm, aperture width (including lip and peristome) 8.6 mm.

Type Locality. Southwest Bay, New Providence [Island, Bahamas], near the landing.

Remarks. This taxon was first illustrated (Maynard, 1920c, fig. 86) as an example of Maynard's "Law of Specific Reincarnation." Maynard (1921b: 140, pl. 37, figs. 1, 2) noted that this taxon was the same size as *S. coryi* (i.e., 1.00 by .40 [inches; 25.4 by 10.2 mm]) and provided colored illustrations. Gould and Woodruff (1986: 474) synonymized this taxon with *Cerion glans* (Küster, 1844).

Taxon 85. *Strophiops inconsueta* **Maynard, 1913c [February 9]: 193–194** [not illustrated in original publication]; Maynard, 1920a, pl. 11, fig. 1; Maynard, 1921b: 142; Maynard, 1924a, pl. 39, figs. 1, 2. Examined 675 specimens. Size given as 1.27 by .50 [inches; 32.3 by 12.7 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 675 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 675 specimens are syntypes. Lot number MCZ 76123 contains a single specimen labeled "Holotype" and a label in Maynard's hand with the term "type," which includes references to subsequently published figures (Maynard, 1924a, pl. 39, figs. 1, 2). This specimen, which approximates the measurements in the original description and the subsequently published illustrations, is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of this taxon. The remaining 674 syntypes, including MCZ 76122, MCZ 177994 (one specimen), and USNM 420051 (75 specimens), become paralectotypes.

Lectotype Measurements. Length 31.9 mm, diameter (excluding lip) 13.7 mm; aperture height (including lip) 11.6 mm, aperture width (including lip and peristome) 11.0 mm.

Type Locality. Southern portion of Great Pimlico [Island, Eleuthera, Bahamas].

Remarks. Clench (1952: 110) considered this taxon to be a valid species and the senior synonym of *S. vetusta* Maynard, 1913 (see Taxon 81).

Taxon 86. *Strophiops transitoria* **Maynard, 1913c [February 9]: 194**; Maynard, 1921b: 141, pl. 37, figs. 9, 10 [not illustrated in original publication]. Examined 250 specimens. Size given as .90 by .35 [inches; 22.9 by 8.9 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 250 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 250 specimens are syntypes. Lot MCZ 117848 contains a single specimen labeled "syntype," whereas MCZ 76119 contained 116 specimens labeled "paratype." All are syntypes, and most appear to be dead collected. Of these, the sequestered specimen (MCZ 117848), which roughly approximates the measurements and subsequent illustration, is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of this taxon. The remaining 249 syntypes, including the 116 specimens in MCZ 76119, become paralectotypes.

Lectotype Measurements. Length 23.2 mm, diameter (excluding lip) 9.6 mm; aperture height (including lip) 9.1 mm, aperture width (including lip and peristome) 7.8 mm.

Type Locality. Northern portion of Great Pimlico [Island, Eleuthera, Bahamas], ranging almost into the area occupied by the foregoing species [*S. inconsueta*].

Remarks. Maynard considered this taxon to be "In the last stage of its specific life" with "only 15 of 250 specimens living, 10 of these young. Both species [*S. inconsueta* and *S. transitoria*] living upon the same food and under the same environment." Maynard (1921b: 141, pl. 37, figs. 9, 10) subsequently added descriptive notes and illustrated this taxon. Clench (1952: 110) listed this taxon as a synonym of *Cerion uniforme* (Maynard, 1913) (see below).

Taxon 87. *Strophiops uniformis* **Maynard, 1913c [February 9]: 194** [not illustrated in original publication]; Maynard, 1921b: 141; Maynard, 1924a, pl. 38, figs. 1, 2. Examined 760 specimens. Size given as 1.15 by .45 [inches; 29.2 by 11.4 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 760 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 760 specimens are syntypes. Lot number MCZ 76117 contains a single specimen labeled "Holotype" that approximates the measurements in the original description and the subsequent illustration in Maynard (1924a, pl. 38, figs. 1, 2). This lot also contains a label in Maynard's hand with the term "Type" that includes references to these figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of this taxon. The remaining 759 syntypes, including MCZ 76118, MCZ 117851, and USNM 420052 (30 specimens), become paralectotypes.

Lectotype Measurements. Length 29.5 mm, diameter (excluding lip) 11.1 mm; aperture height (including lip) 10.9 mm, aperture width (including lip and peristome) 9.9 mm.

Type Locality. Little Pimlico [Island, Eleuthera, Bahamas].

Remarks. Maynard (1921b: 141, 1924a, pl. 38, figs. 1, 2) subsequently added descriptive notes and illustrated this taxon. Clench (1952: 110) listed this as a valid species but did not mention type specimens.

Taxon 88. *Strophiops hyattii* **Maynard, 1913c [February 9]: 194–195** [not illustrated in original publication]; Maynard, 1921b: 142; Maynard, 1926, pl. 42, figs. 1, 2. Examined 600 specimens. Measurements not provided.

Type Material. The original description

did not distinguish among the 600 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 600 specimens are syntypes. Lot number MCZ 76133 contains a single specimen labeled "holotype." No measurements were provided in the original description, but this specimen approximates the measurements (1.10 by .45 [inches; 27.9 by 14.0 mm]) and illustration in Maynard (1921b: 142, 1926, pl. 42, figs. 1, 2) [as *S. hyatiii*]. This lot also contains a label in Maynard's hand with the term "type," which includes references to these figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of this taxon. The remaining 599 syntypes, including MCZ 76134, MCZ 118036 (one specimen), and USNM 419973 (75 specimens), become paralectotypes.

Lectotype Measurements. Length 26.3 mm, diameter (excluding lip) 11.0 mm; aperture height (including lip) 9.8 mm, aperture width (including lip and peristome) 9.3 mm.

Type Locality. Bar Bay Settlement, Current Island [Eleuthera, Bahamas].

Remarks. Clench (1952: 109) listed this taxon as a valid species.

Taxon 89. *Strophiops vetustapraedevina* **Maynard, 1913c [February 9]: 195** [not illustrated]. Examined 50 specimens. Size given as 1.15 by .48 [inches; 29.2 by 12.2 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 50 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 50 specimens are syntypes. This taxon was not represented in the collections of the MCZ, nor was it present in Maynard's collection at the time it was acquired from his daughter, as revealed by an examination of the MCZ catalog. Three syntypes of this taxon, which Bartsch purchased from Maynard in 1923, were located in the USNM collection. Of these, the best preserved specimen (USNM 359439) is selected as the lectotype. The 49 syntypes, including the two specimens in USNM 359438, become paralectotypes.

Lectotype Measurements. Length 31.7 mm, diameter (excluding lip) 13.6 mm; aperture height (including lip) 13.5 mm, aperture width (including lip and peristome) 11.1 mm.

Type Locality. Fossil on Great Pimlico [Island, Eleuthera, Bahamas].

Remarks. Following Article 32.5.2.4 (ICZN, 1999: 40), the hyphen is removed from *vetusta-praedevina* and the taxon becomes *vetustapraedevina.* Also reported from Upper Fleming and the Silver Keys. Clench (1952: 110, 1957: 167) listed this taxon as a synonym of *Cerion inconsuetum* (Maynard, 1913).

Taxon 90. *Strophiops praedivina* **Maynard, 1913c [February 9]: 196** [not illustrated in original publication]; Maynard, 1921b: 141, pl. 37, figs. 5, 6. Examined 100 specimens. Size given as 1.05 by .45 [inches; 26.7 by 11.4 mm], but the term "type" was not used.

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Figures 87–99. Taxon 87. *Strophiops uniformis* Maynard, 1913. Lectotype MCZ 76117. Little Pimlico Island, Eleuthera, Bahamas. Taxon 88. *Strophiops hyattii* Maynard, 1913. Lectotype MCZ 76133. Bar Bay Settlement, Current Island, Eleuthera, Bahamas. Taxon 89. *Strophiops vetustapraedevina* Maynard, 1913. Lectotype USNM 359439. Fossil on Great Pimlico Island, Eleuthera, Bahamas. Taxon 90. *Strophiops praedivina* Maynard, 1913. Lectotype MCZ 76346. Upper Fleming Key, 20 miles NE of New Providence Island, Bahamas. Taxon 91. *Strophiops praedivinauniversa* Maynard, 1913. [Not illustrated.] The lectotype (MCZ 76287) of *Strophiops universa* Maynard, 1913 [Taxon 92], is designated as the neotype of *Strophiops praedivinauniversa* Maynard, 1913, making *Strophiops praedivinauniversa* Maynard, 1913, an objective junior synonym of *Strophia universa* Maynard, 1913. Taxon 92. *Strophiops universa* Maynard, 1913. Lectotype MCZ 76287. Fossil on Green Key, Rose Island, New Providence Island, Bahamas. Taxon 93. *Strophiops exigua* Maynard, 1913. Lectotype MCZ 76357. Southern portion of Fleming

Key, 20 miles NE of New Providence Island, Bahamas. Taxon 94. *Strophiops multa* Maynard, 1913. Lectotype MCZ 76354. Northern portion of Fleming Key, 20 miles NE of New Providence Island, Bahamas. Taxon 95. *Strophiops obliterata* Maynard, 1913. Lectotype MCZ 76334. Booby Rock, 16 miles NE of New Providence Island, Bahamas. Taxon 96. *Strophiops ornatula* Maynard, 1913. Lectotype MCZ 76343. Current Settlement, Eleuthera, Bahamas. Taxon 97. *Strophiops ornatulaclappii* Maynard, 1913. Lectotype MCZ 117738. North of the Current Settlement, Eleuthera, Bahamas. Taxon 98. *Strophiops clappii* Maynard, 1913. Lectotype MCZ 76344. Salina, north of the Current Settlement, Eleuthera, Bahamas. Taxon 99. *Strophiops ornatularufina* Maynard, 1913. Lectotype MCZ 118095. South of the Current Settlement, Eleuthera, Bahamas.

Type Material. The original description did not distinguish among the 100 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 100 specimens are syntypes. Lot number MCZ 76346 contains a single specimen labeled "holotype." This lot also contains a label in Maynard's handwriting with the name of the taxon and the term "type." This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of this taxon. The remaining 99 syntypes, including MCZ 76347 (62 specimens), become paralectotypes.

Lectotype Measurements. Length 27.7 mm, diameter (excluding lip) 11.2 mm; aperture height (including lip) 10.4 mm, aperture width (including lip and peristome) 8.9 mm.

Type Locality. Upper Fleming [Key, 20 miles NE of New Providence Island, Bahamas].

Remarks. A fossil taxon also reported from Lower Fleming and Great Pimlico. Maynard (1921b: 141, pl. 37, figs. 5, 6) subsequently provided illustrations and a different measurement (1.08 by .55 [inches; 27.4 by 14.0 mm]) and reported only 55 specimens. The taxon is spelled *praedivina* in the original description and subsequent plate caption, but as *predivina* in Maynard (1921b: 141) and in the sales catalog (Maynard, 1924?: [6]). Clench (1952: 109) listed this taxon as a synonym of *Cerion exiguum* (Maynard, 1913).

Taxon 91. *Strophiops praedivinauniversa* **Maynard, 1913c [February 9]: 196** [not illustrated]. Examined 25 specimens. Measurements not provided.

Type Material. The original description did not distinguish among the 25 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 25 specimens are syntypes. This taxon was not represented in the collections of the MCZ, nor was it present in Maynard's collection at the time it was acquired from his daughter, as revealed by an examination of the MCZ catalog. This taxon was not among the material purchased for the USNM collections either during Maynard's lifetime or from his estate. Searches of the collections and/or databases of The Academy of Natural Sciences of Philadelphia, The Field Museum of Natural History, The Florida Museum of Natural History, and The Museum of Biological Diversity, The Ohio State University, failed to uncover a single specimen catalogued under this name. This taxon was never illustrated, nor did it appear in any of Maynard's subsequent publications or catalogs. The description is limited to the statement "Intermediate between *pdrœivina* [sic] and *universa,* but inclined to be more like the latter." No specimens bearing the name *Strophiops praedivinauniversa* could be located in museums, nor could this taxon be identified on the basis of its limited description. The lectotype of *Strophiops universa* Maynard, 1913 (MCZ 76287), is here designated as the neotype of *Strophiops praedivinauniversa* Maynard, 1913, making *Strophiops praedivinauniversa* Maynard, 1913, an objective synonym of *Strophia universa* Maynard, 1913.

Type Locality. Maynard (1913c: 194) noted that *S. praedivinauniversa* occurred on Upper Fleming [Key, 20 miles NE of New Providence Island, Bahamas], both living and fossil. Although *S. universa* was reported from Upper Fleming, Great Pimlico, and the northern end of Rose Island, the type locality of *S. universa,* and therefore of *S. praedivinauniversa,* is Green Key, New Providence Island, Bahamas, per Article 76.3 (ICZN, 1999: 87).

Remarks. Following Article 32.5.2.4 (ICZN, 1999: 40), the hyphen is removed from *praedivina-universa* and the taxon becomes *praedivinauniversa.* Clench (1952: 109) listed this taxon as a synonym of *Cerion exiguum* (Maynard, 1913).

Taxon 92. *Strophiops universa* **Maynard, 1913c [February 9]: 196** [not illustrated in original publication]; Maynard, 1921b: 140, pl. 37, figs. 3, 4. Examined 30 specimens. Size given as .55 by .32 [inches; 14.0 by 8.1 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 30 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 30 specimens are syntypes.

MCZ 76287, labeled "Paratype," contained 26 specimens (many fragmentary), of which one was sequestered, together with a label in Maynard's handwriting with the taxon name and "Plate 37, figs. 3–4." The sequestered specimen closely approximates the subsequently published illustration and published width measurement. The published length measurement is either in error, or incorporates length measurements of fragmentary specimens. The sequestered specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of this taxon. The remaining 25 specimens, recatalogued as MCZ 356475, are among the 29 syntypes that become paralectotypes.

Lectotype Measurements. Length 18.9 mm, diameter (excluding lip) 8.2 mm; aperture height (including lip) 8.2 mm, aperture width (including lip and peristome) 6.3 mm.

Type Locality. Fossil on Green Key [New Providence Island, Bahamas].

Remarks. Also reported from Upper Fleming, Great Pimlico, and northern end of Rose Island. Maynard (1913c: 196) surmised that "The wide range of this little species suggests that the islands on which it is now found were once connected." Maynard (1921b: 140, pl. 37, figs. 3, 4) subsequently provided illustrations of this taxon and listed 50 specimens examined. It is unclear whether he later collected additional specimens or whether the number is a typographical error. Clench (1952: 110) listed this taxon as a synonym of *Cerion uniforme* (Maynard, 1913).

Taxon 93. *Strophiops exigua* **Maynard, 1913c [February 9]: 196** [not illustrated in original publication]; Maynard, 1921b: 141; Maynard, 1924a, pl. 38, figs. 3, 4. Examined 1,000 specimens. Size given as 1.30 by 50 [sic .50] [inches; 33.0 by 12.7 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 1,000 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 1,000 specimens are syntypes. Lot MCZ 76357 contains a single specimen labeled "Holotype." This specimen approximates the measurements in the original description and the illustration in Maynard (1921b: 141, 1924a, pl. 38, figs. 3, 4). This lot also contains a label in Maynard's hand with the term "type," which includes references to these figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of this taxon. The remaining 999 syntypes, including MCZ 76356 (171 specimens), MCZ 117837 (1 specimen), and USNM 420011 (250 specimens), become paralectotypes.

Lectotype Measurements. Length 31.3 mm, diameter (excluding lip) 11.6 mm; aperture height (including lip) 10.7 mm, aperture width (including lip and peristome) 9.1 mm.

Type Locality. Southern portion of Fleming Key [20 miles NE of New Providence Island, Bahamas].

Remarks. This taxon was reported from living specimens, which were abundant, and from fossils in the limestone, which were rare. Maynard (1921b: 141, 1924a, pl. 38, figs. 3, 4) provided descriptive notes and illustrations of this taxon. Clench

(1952: 109) listed this taxon as a valid species.

Taxon 94. *Strophiops multa* **Maynard, 1913c [February 9]: 197** [not illustrated in original publication]; Maynard, 1921b: 141; Maynard, 1924a, pl. 38, figs. 5, 6. Examined 964 specimens. Size given as 1.10 by .40 [inches; 27.9 by 10.2 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 964 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 964 specimens are syntypes. Lot number MCZ 76354 contains a single specimen labeled "Holotype." This specimen approximates the measurements in the original description (within 5%) and the illustration in Maynard (1924a, pl. 38, figs. 5, 6). This lot also contains a label in Maynard's hand with the term "type," which includes references to these figures (as pl. 38, figs. 7, 8). This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of this taxon. The remaining 963 syntypes, including MCZ 76355 and MCZ 118069, become paralectotypes.

Lectotype Measurements. Length 28.9 mm, diameter (excluding lip) 10.8 mm; aperture height (including lip) 10.6 mm, aperture width (including lip and peristome) 9.0 mm.

Type Locality. Northern portion of Fleming Key [20 miles NE of New Providence Island, Bahamas].

Remarks. Maynard (1921b: 141, 1924a, pl. 38, figs. 5, 6) provided additional descriptive notes and illustrations of this taxon. Clench (1934: 214) initially considered this to be a valid species, but later (1952: 109) listed this taxon as a synonym of *Cerion exiguum* (Maynard, 1913). Gould and Woodruff (1986: 474) synonymized this taxon with *C. glans* (Küster, 1844).

Taxon 95. *Strophiops obliterata* **Maynard, 1913c [February 9]: 197** [not illustrated in original publication]. Examined 812 specimens. Size given as 1.15 by .30 [inches; 29.2 by 7.6 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 812 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 812 specimens are syntypes. There were no specimens of *S. obliterata* Maynard, 1913, in the collections of the MCZ, nor were there any entries corresponding to this taxon in the MCZ catalog either during Maynard's life or among the specimens purchased from his estate. Maynard and Clapp (1915: 191) recognized that *S. obliterata* Maynard, 1913, was a homonym of *Strophia scripta obliterata* Maynard, 1896, and proposed the replacement name *Strophiops sula* [Taxon 105]. Lot number MCZ 76334 contains a single specimen labeled as the "Holotype" of *S. sula.* Because *Strophiops obliterata* Maynard, 1913, was based on 812 syntypes, this specimen is here designated as the lectotype of *Strophiops obliterata* Maynard, 1913, and consequently [Article 72.7, ICZN, 1999: 78] its replacement name, *Strophiops sula* Maynard and Clapp, 1915. Lots MCZ 76335 (170 specimens) and USNM 420096 (125 specimens) contain numerous specimens labeled as paralectotypes of *S. sula.* These specimens are paralectotypes of *S. obliterata* Maynard, 1913, as well as of its replacement name *S. sula.*

Lectotype Measurements. Length 31.8 mm, diameter (excluding lip) 12.4 mm; aperture height (including lip) 12.3 mm, aperture width (including lip and peristome) 10.1 mm.

Type Locality. Booby Rock [16 miles NE of New Providence Island, Bahamas].

Remarks. Although the taxon was never illustrated as *S. obliterata* Maynard, 1913, Maynard (1921b: 142, 1924a, pl. 38, figs. 7, 8) subsequently published additional

notes and illustrations of *S. sula.* Gould and Woodruff (1986: 474) listed both *S. obliterata* Maynard, 1913, and *S. sula* Maynard and Clapp, 1915, as synonyms of *Cerion glans* (Küster, 1844).

Taxon 96. *Strophiops ornatula* **Maynard, 1913c [February 9]: 197–198** [not illustrated in original publication]; Maynard, 1919a, pl. 6, fig. 4; Maynard, 1919b, fig. 11. Examined 3,528 specimens. Size given as 1.15 by .30 [inches; 29.2 by 7.6 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 3,528 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 3,528 specimens are syntypes. Clench (1934: 217) mentioned comparing the types of *Cerion ornatula* (Maynard) and *C. laeve* Plate, but did not specify the sort of type, nor the repository or catalog number of the type lot. Later, Clench (1952: 112) listed MCZ 76343 as the holotype of *C. ornatula.* This lot contains a single specimen labeled "Holotype" that approximates the published length but not the width and is similar to the subsequently published illustration of this taxon (Maynard, 1919a, pl. 6, fig. 4). This specimen, which is accompanied by a label in Maynard's hand that includes the term "type" and references to these illustrations, cannot be a holotype, nor can Clench's listing be accepted as a lectotype designation (Article 74.5, ICZN, 1999: 83). This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original, or at least subsequent concept of it. The remaining 3,527 syntypes, including MCZ 76342 and USNM 420137 (400 specimens), become paralectotypes.

Lectotype Measurements. Length 22.4 mm, diameter (excluding lip) 9.0 mm; aperture height (including lip) 8.9 mm, aperture width (including lip and peristome) 7.1 mm.

Type Locality. Current Settlement [Eleuthera, Bahamas].

Remarks. This taxon was later illustrated (Maynard, 1919a, pl. 6, fig. 3, 1919b, fig. 11). Clench (1934: 217) reported that *Cerion ornatula* "is an absolute synonym" of *C. laeve* (Plate, 1907) on the basis of comparisons of type material.

Taxon 97. *Strophiops ornatulaclappii* **Maynard, 1913c [February 9]: 198** [not illustrated in original publication]; Maynard, 1921b: 153. Examined 50 specimens. Measurements not provided.

Type Material. The original description did not distinguish among the 50 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 50 specimens are syntypes. There were no entries for this taxon in the MCZ catalog, indicating that this taxon was not represented in Maynard's collection at the time of his death. Lot number MCZ 117738 contained nine specimens from the collection of N. A. Clapp, Maynard's collaborator and co-author. Because neither measurements nor illustration were published, an adult specimen is selected to serve the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining eight specimens were recatalogued as MCZ 356993 and are among the 49 syntypes that become paralectotypes.

Lectotype Measurements. Length 20.3 mm, diameter (excluding lip) 8.3 mm; aperture height (including lip) 7.9 mm, aperture width (including lip and peristome) 6.5 mm.

Type Locality. Living just north of the Current Settlement [Eleuthera, Bahamas].

Remarks. Following Article 32.5.2.4 (ICZN, 1999: 40), the hyphen is removed from *ornatula-clappii* and the taxon becomes *ornatulaclappii.* Clench (1952: 111) listed this taxon in the synonymy of *Cerion laeve* Plate, 1907, citing it as a nomen nudum.

Taxon 98. *Strophiops clappii* **Maynard, 1913c [February 9]: 198** [not illustrated in original publication]; Maynard, 1919a, fig. 10, pl. 6, fig. 5; Maynard, 1921b: 153, pl. 48, fig. 6 [plate never issued]. Number of specimens examined not given, but Maynard (1913c: 198) stated the fields contained "absolutely millions of dead shells of this [species]." Size given as .50 by .20 [inches; 12.7 by 5.1 mm], but the term "type" was not used. Maynard (1921b: 153) listed 2,000 specimens.

Type Material. The original description did not provide the number of specimens examined, nor is there mention of type material in the other parts of this publication. Thus, there are an unspecified number of syntypes, but not more than the 2,000 specimens mentioned by Maynard (1921b: 153). Clench (1952: 112) listed MCZ 76344 as the "Holotype." Lot MCZ 76344 was labeled "holotype" and accompanied by a note in Maynard's handwriting identifying the taxon and containing the term "Type" as well as references to both published and unpublished illustrations. This specimen is nearly identical to the published illustration and measurements. It is here selected as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 1,999 syntypes, including MCZ 76345 and MCZ 21128, become paralectotypes.

Lectotype Measurements. Length 12.6 mm, diameter (excluding lip) 5.1 mm; aperture height (including lip) 4.4 mm, aperture width (including lip and peristome) 3.8 mm.

Type Locality. Living on a salina north of the Current Settlement [Eleuthera, Bahamas].

Remarks. This taxon was illustrated by Maynard (1919a, fig. 10, pl. 6, fig. 5 [as *clappi*]). Clench (1952: 111) listed this taxon in the synonymy of *Cerion laeve* Plate, 1907.

Taxon 99. *Strophiops ornatularufina* **Maynard, 1913c [February 9]: 198** [not illustrated in original publication]. Examined 50 specimens. Measurements not provided.

Type Material. The original description did not distinguish among the 50 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 50 specimens are syntypes. There were no entries for this taxon in the MCZ catalog, indicating that this taxon was not represented in Maynard's collection at the time of his death. Lot number MCZ 118095 contains a single specimen from the collection of N. A. Clapp, Maynard's collaborator and co-author. This specimen, one of the 50 syntypes, is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 49 syntypes become paralectotypes.

Lectotype Measurements. Length 19.5 mm, diameter (excluding lip) 8.2 mm; aperture height (including lip) 7.5 mm, aperture width (including lip and peristome) 6.9 mm.

Type Locality. South of the Current Settlement [Eleuthera, Bahamas].

Remarks. Following Article 32.5.2.4 (ICZN, 1999: 40), the hyphen is removed from *ornatula-rufina* and the taxon becomes *ornatularufina.*

Taxon 100. *Strophiops rufina* **Maynard, 1913c [February 9]: 198** [not illustrated]; Maynard, 1924a: 153, pl. 48, figs. 9, 10 [plate never published]. Examined 20 specimens. Size given as .75 by .40 [inches; 19.0 by 10.2 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 20 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 20 specimens are syntypes. Lot MCZ 76304 contains a single

specimen labeled "Holotype" that roughly approximates the measurements of this taxon. It is accompanied by a label in Maynard's hand with the term "type," which includes references to figures that were never published. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 19 syntypes, including MCZ 76303, become paralectotypes.

Lectotype Measurements. Length 19.2 mm, diameter (excluding lip) 8.5 mm; aperture height (including lip) 7.9 mm, aperture width (including lip and peristome) 6.9 mm.

Type Locality. Rare south of the Current Settlement [Eleuthera, Bahamas].

Remarks. Clench (1952: 109) listed this taxon as a synonym of *Cerion hyattii* (Maynard, 1913).

Taxon 101. *Strophiops tabida* **Maynard, 1913c [February 9]: 199** [not illustrated in original publication]; Maynard, 1921b: 152 [as *tibida*], pl. 44, figs. 9, 10 [illustrations never published].

Type Material. Because the original description did not mention the number of specimens examined, this taxon is based on an unspecified number of syntypes. Maynard (1921b: 152) subsequently reported 100 specimens examined and gave the size as 1.00 by .40 [inches; 25.4 by 10.2 mm]. Lot MCZ 76024 contains a single specimen labeled "Holotype" that closely approximates the subsequently published measurements for this taxon. This lot also contains a label in Maynard's hand with the term "Type" that includes references to illustrations that were never published. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of this taxon. The remaining syntypes (≤99), including MCZ 76025, become paralectotypes.

Lectotype Measurements. Length 25.6 mm, diameter (excluding lip) 10.3 mm; aperture height (including lip) 9.3 mm, aperture width (including lip and peristome) 8.1 mm.

Type Locality. West shore of Eleuthera [Bahamas] near the Current Settlement, living on rocks close by the sea.

Remarks. Maynard (1913c: 199) noted, "Some individuals appear to mimic species unknown to me. The most remarkable recessional species that I have thus far found as, all things considered, it is the most remote phylogenetically from the species it mimics." Clench (1952: 109) listed this taxon as a synonym of *Cerion hyattii* (Maynard, 1913).

Taxon 102. *Strophiops helena* **Maynard, 1914 [August 18]: 177–179, figs. 8A, B, C, D.** Examined 1,000 specimens. Size given as .92 by .43 [inches; 23.4 by 10.9 mm], but the term "type" was not used in connection with the measurements. Caption to text fig. 8, "STROPHIOPS HELENA: A, front. B, side view of type; c, front of aperture of type enlarged × 2; D, margin of senescent specimen × 2."

Type Material. The original description identifies a single type specimen, the holotype, in the figure captions. Lot MCZ 76216 contains a single specimen labeled "Holotype." This specimen is accompanied by a label in Maynard's hand containing the term "Type" and also giving the correct species number and plate number but incorrect volume and page for this taxon in Maynard (1921b: 131, pl. 7, figs. 5–8). Specimen MCZ 76216 is the originally designated holotype of *Strophiops helena* Maynard, 1914. The remaining 999 specimens, including MCZ 76203 (231 specimens) and USNM 419990 (100 specimens), are paratypes.

Holotype Measurements. Length 22.6 mm, diameter (excluding lip) 10.1 mm; aperture height (including lip) 8.4 mm, aperture width (including lip and peristome) 7.8 mm.

Type Locality. Fields directly south of Fresh Creek, Andros [Bahamas].

Remarks. Maynard (1919b, pl. 7, figs. 5–8) re-illustrated this taxon.

Taxon 103. *Strophiops thompsoni* **Maynard and Clapp, 1915 [February 8]: 179 bis** [not illustrated in original publication]; Maynard, 1921b: 139, pl. 35, figs. 9, 10. Examined 20 specimens. Size given as 1.05 by .45 [inches; 26.7 by 11.4 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 20 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 20 specimens are syntypes. Lot MCZ 76186 contains a single specimen labeled "Holotype." This specimen closely approximates the measurements in the original description and the subsequent illustrations (Maynard, 1921b, pl. 35, figs. 9, 10) and is accompanied by a label in Maynard's hand containing the term "Type" that refers to the published figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. Lot MCZ 76187 contains 264 specimens (most damaged, incomplete, or juvenile) and was labeled "paratype." Because Maynard added specimens after publishing the description, it is not clear which 19 of the 264 specimens are paralectotypes.

Lectotype Measurements. Length 25.7 mm, diameter (excluding lip) 11.3 mm; aperture height (including lip) 10.0 mm, aperture width (including lip and peristome) 8.5 mm.

Type Locality. Occurs as a fossil in the rock on the south shore of Hog Island [= Paradise Island, Nassau, New Providence Island, Bahamas].

Remarks. Maynard (1921b: 139, pl. 35, figs. 9, 10) provided additional descriptive information and illustrations, noting 370 specimens in his collection. Gould and Woodruff (1986: 482) provisionally attributed this taxon to *Cerion glans* (Küster, 1844).

Taxon 104. *Strophiops morula* **Maynard and Clapp, 1915 [February 8]: 179 bis-180 bis** [not illustrated in original publication]; Maynard, 1921b: 139, pl. 36, figs. 1, 2. Neither the number of specimens examined nor measurements are provided in the original description.

Type Material. The original description did not specify the number of specimens examined. In the subsequent monograph, Maynard (1921b: 139, pl. 36, figs. 1, 2) listed 60 specimens. The size of the syntype lot is uncertain, but does not exceed 60 syntypes. The original description provided neither measurements nor illustration but stated that there were 10 whorls, with 23 costae on the final whorl. Lot number MCZ 76017 contains a single specimen labeled "Holotype." This specimen consists of nine whorls but has 23 costae on the final whorl. This specimen is accompanied by a label in Maynard's hand with the term "type," which includes references to the subsequently published figures. However, it does not closely match either the figures

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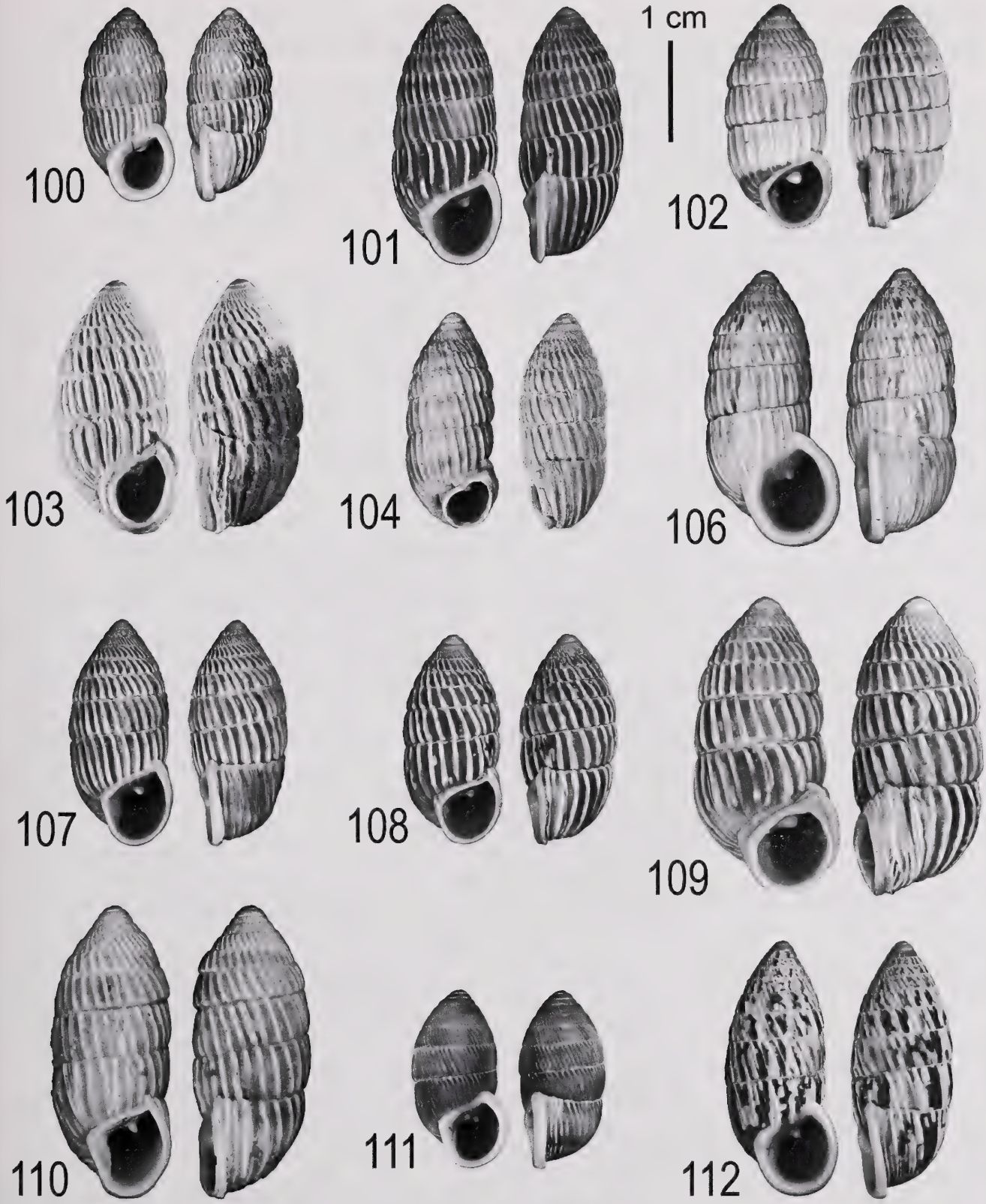
Figures 100–113. Taxon 100. *Strophiops rufina* Maynard, 1913. Lectotype MCZ 76304. South of the Current Settlement Eleuthera, Bahamas. Taxon 101. *Strophiops tabida* Maynard, 1913. Lectotype MCZ 76024. Near the Current Settlement, west shore of Eleuthera, Bahamas. Taxon 102. *Strophiops helena* Maynard, 1914. Holotype MCZ 76216. Fields directly south of Fresh Creek, Andros, Bahamas. Taxon 103. *Strophiops thompsoni* Maynard and Clapp, 1915. Lectotype MCZ 76186. Fossil, south shore of Hog Island [Paradise Island], Nassau, New Providence Island, Bahamas. Taxon 104. *Strophiops morula* Maynard and Clapp, 1915. Lectotype MCZ 76017. Spruce Key, 4 miles E of Nassau, New Providence Island, Bahamas. Taxon 105. *Strophiops sula* Maynard and Clapp, 1915. [Not illustrated.] Replacement name for *Strophiops obliterata* Maynard, 1913 [Taxon 95], a junior homonym of *S. scripta obliterata* Maynard, 1896 [Taxon 53]. The type specimens and type locality of *S. obliterata* Maynard, 1913 are also the type specimens and type locality of *S. sula* Maynard and Clapp, 1915. Taxon 106. *Strophiops hesternia* Maynard and Clapp, 1915. Lectotype MCZ 76157. West end of Booby Rock, 16 miles NE of New Providence Island, Bahamas.



Taxon 107. *Strophiops caerulea* Maynard and Clapp, 1915. Lectotype MCZ 76308. Field north of Ft. Charlotte, Nassau, New Providence Island, Bahamas. Taxon 108. *Strophiops devereuxi* Maynard and Clapp, 1915. Lectotype MCZ 76137. Devereux Estate west end of New Providence Island, Bahamas. Taxon 109. *Strophiops praedicta* Maynard and Clapp, 1915. Lectotype MCZ 76393. Great Pimlico Island, Eleuthera, Bahamas. Taxon 110. *Strophiops prisca* Maynard and Clapp, 1915. Lectotype 76353. Fossil in the rocks on east end of Salt Key, New Providence Island, Bahamas. Taxon 111. *Strophiops tenui* Maynard and Clapp, 1915. Lectotype MCZ 76350. East end of New Providence Island, Bahamas. Taxon 112. *Strophiops fulminea* Maynard and Clapp, 1915. Lectotype MCZ 76276. Rocky shore east of Ft. Winton, New Providence Island, Bahamas. Taxon 113. *Strophiops longidentata* Maynard, 1919. Nomen nudum. [Not illustrated.]

or the measurements in the monograph. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining syntypes (≤59), including MCZ 76018, become paralectotypes.

Lectotype Measurements. Length 21.6 mm, diameter (excluding lip) 8.8 mm; aperture height (including lip) 7.7 mm, aperture width (including lip and peristome) 5.7 mm.

Type Locality. Spruce Key [4 miles E of Nassau, New Providence Island, Bahamas].

Remarks. Semi-fossil. Maynard (1921b: 139, pl. 36, figs. 1, 2) provided additional descriptive information, including measurements [1.10 by .50 inches; 27.9 by 12.7 mm] as well as illustrations. Gould and Woodruff (1986: 474) synonymized this taxon with *Cerion glans* (Küster, 1844).

Taxon 105. *Strophiops sula* **Maynard and Clapp, 1915 [February 8]: 180 bis.** Replacement name for *Strophiops obliterata* Maynard, 1913 [Taxon 95], a junior secondary homonym of *Strophia scripta obliterata* Maynard, 1896 [Taxon 53].

Type Material. The type specimens and type locality of *S. obliterata* Maynard, 1913 [Taxon 95], are also the type specimens of *S. sula* Maynard and Clapp, 1915.

Remarks. Strophiops obliterata Maynard, 1913, was not illustrated, nor was *S. sula* Maynard and Clapp, 1915, at the time of its publication. Maynard (1921b: 142, 1924a, pl. 38, figs. 7, 8) subsequently published additional notes and illustrations of *S. sula.* Gould and Woodruff (1986: 474) synonymized this taxon with *Cerion glans* (Küster, 1844).

Taxon 106. *Strophiops hesternia* **Maynard and Clapp, 1915 [February 8]: 180 bis** [not illustrated in original publication]; Maynard, 1921b: 142; Maynard, 1924a, pl. 38, figs. 9, 10. Examined 200 specimens. Measurements not provided.

Type Material. The original description did not distinguish among the 200 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 200 specimens are syntypes. No specimen labeled "Holotype" was located at the MCZ. An examination of the MCZ catalog revealed that no specimen identified as "type" was present in Maynard's collection at the time of its sale. Lot number MCZ 76157 contained 27 specimens labeled "paratypes" together with a note in Maynard's handwriting listing the taxon name and locality, but lacking the word "type" or references to the illustrations. Gould and Woodruff (1986: 474) reported examining "paratypes" but did not see a "holotype." One of these specimens, which most closely matches Maynard's only illustration of this taxon in size and proportions, is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of it. The remaining 26 specimens were recatalogued as MCZ 356994 and are among the 199 syntypes that become paralectotypes.

Lectotype Measurements. Length 27.9 mm, diameter (excluding lip) 11.6 mm; aperture height (including lip) 11.2 mm, aperture width (including lip and peristome) 9.6 mm.

Type Locality. West end of Booby Rock [16 miles NE of New Providence Island, Bahamas] by a low place over which the sea frequently breaks.

Remarks. Gould and Woodruff (1986: 474) synonymized this taxon with *Cerion glans* (Küster, 1844).

Taxon 107. *Strophiops caerulea* **Maynard and Clapp, 1915 [February 8]: 181** [not illustrated in original publication]; Maynard, 1921b: 140, pl. 36, figs. 7, 8. Examined 50 specimens. Size given as .92 by .40 [inches; 23.4 by 10.2 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 50 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 50 specimens are syntypes. Lot number MCZ 76308 contains a single specimen labeled "Holotype" that approximates the illustration and the measurements of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to subsequently published figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 49 syntypes become paralectotypes.

Lectotype Measurements. Length 22.8 mm, diameter (excluding lip) 10.1 mm; aperture height (including lip) 9.0 mm, aperture width (including lip and peristome) 7.5 mm.

Type Locality. In field N of Ft. Charlotte, Nassau [New Providence Island, Bahamas].

Remarks. Maynard considered this taxon to be extinct at the time it was described. This taxon was subsequently illustrated (Maynard, 1921b, pl. 36, figs. 7, 8). Gould and Woodruff (1986: 474) synonymized this taxon with *Cerion glans* (Küster, 1844).

Taxon 108. *Strophiops devereuxi* **Maynard and Clapp, 1915 [February 8]: 181** [not illustrated in original publication]; Maynard, 1921b: 140, pl. 36, figs. 9, 10. Unspecified number of specimens examined. Size given as .85 by .40 [inches; 21.6 by 10.2 mm], but the term "type" was not used.

Type Material. The original description did not specify the number of specimens examined. In the subsequent monograph, Maynard (1921b: 140) lists 164 specimens. The size of the syntype lot is uncertain but does not exceed 164 syntypes. Lot number MCZ 76137 contains a single specimen labeled "Holotype" that approximates the measurements and subsequently published illustration of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining syntypes (≤163), including MCZ 76138 and MCZ 117730 (one specimen), become paralectotypes.

Lectotype Measurements. Length 20.9 mm, diameter (excluding lip) 9.7 mm; aperture height (including lip) 8.4 mm, aperture width (including lip and peristome) 6.9 mm.

Type Locality. Devereux Estate west end of New Providence [Island, Bahamas].

Remarks. This taxon was later listed as *S. deveruxi* (Maynard, 1921b: 140) and *S. devereuaxi* (Maynard, 1924?: [7]) and illustrated under its correct original spelling (Maynard, 1921b, pl. 36, figs. 9, 10). Gould and Woodruff (1986: 475) synonymized this taxon with *Cerion glans* (Küster, 1844).

Taxon 109. *Strophiops praedicta* **Maynard and Clapp, 1915 [February 8]: 181** [not illustrated]. Number of specimens not specified; measurements not provided.

Type Material. The original description did not specify the number of specimens examined. This taxon does not appear in any of Maynard's subsequent publications or catalogs. The size of the type series is uncertain. An examination of the MCZ catalog revealed that no specimen identified as "type" was present in Maynard's collection at the time of its sale. Lot MCZ 76393 contains 91 specimens (many damaged, incomplete, or juvenile) and was labeled "paratype." Because no characteristics were provided by which an individual specimen could be identified, a large, mature, complete specimen is selected from

the syntype series to serve as lectotype to provide an objective standard of reference for this species-group taxon. The remaining 90 specimens were recatalogued as MCZ 356995 and are paralectotypes.

Lectotype Measurements. Length 29.5 mm, diameter (excluding lip) 13.4 mm; aperture height (including lip) 11.3 mm, aperture width (including lip and peristome) 10.0 mm.

Type Locality. Great Pimlico [Island, Eleuthera, Bahamas].

Remarks. Fossil in the rocks. Clench (1952: 110) listed this taxon as a synonym of *Cerion uniforme* (Maynard, 1913).

Taxon 110. *Strophiops prisca* **Maynard and Clapp, 1915 [February 8]: 182** [not illustrated in original publication]; Maynard, 1921b: 143; Maynard, 1924a, pl. 39, figs. 5, 6. Unspecified number of specimens examined. Size given as 1.15 by .45 [inches; 29.2 by 11.4 mm], but the term "type" was not used.

Type Material. The original description did not specify the number of specimens examined. In the subsequent monograph, Maynard (1921b: 143) lists 15 specimens. The size of the syntype lot is uncertain but does not exceed 15 syntypes. Lot MCZ 76353 contains a single specimen labeled "Holotype" that approximates the measurements of this taxon as well as the subsequently published illustrations. This specimen is accompanied by a label in Maynard's hand with the term "type," which includes references to these illustrations. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining syntypes (≤14), including MCZ 76352, become paralectotypes.

Lectotype Measurements. Length 29.3 mm, diameter (excluding lip) 11.7 mm; aperture height (including lip) 10.7 mm, aperture width (including lip and peristome) 7.9 mm.

Type Locality. Fossil in the rocks on east end of Salt Key [New Providence Island, Bahamas].

Remarks. Maynard (1921b: 143, 1924a, pl. 39, figs. 5, 6) noted 15 specimens and provided illustrations for this taxon. Gould and Woodruff (1986: 482) synonymized this taxon with *Cerion glans* (Küster, 1844).

Taxon 111. *Strophiops tenui* **Maynard and Clapp, 1915 [February 8]: 182** [not illustrated in original publication]; Maynard, 1921b: 149–150, pl. 46, figs. 1, 2 [pl. 46 was never issued]. Unspecified number of specimens examined. Size given as .70 by .33 [inches; 17.8 by 8.4 mm], but the term "type" was not used.

Type Material. The original description did not specify the number of specimens examined. In the subsequent monograph, Maynard (1921b: 150) lists 600 specimens. The size of the syntype lot is uncertain, but does not exceed 600 syntypes. Lot MCZ 76350 contains a single specimen labeled "Holotype" that approximates the measurements of this taxon. This specimen is accompanied by a label in Maynard's hand with the term "type," which includes references to illustrations that were never published. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining syntypes (≤599), including MCZ 76351, become paralectotypes.

Lectotype Measurements. Length 17.6 mm, diameter (excluding lip) 8.5 mm; aperture height (including lip) 7.8 mm, aperture width (including lip and peristome) 6.8 mm.

Type Locality. Isolated on a portion of shore on east end of New Providence [Island, Bahamas].

Remarks. Maynard and Clapp (1915: 182) considered this taxon to be extinct at the time it was described, but later, May-

nard (1921b: 149–150) wrote that they were common along a short reach of shore just west of East Point Light, New Providence, and that 600 specimens were collected, chiefly dead. Gould and Woodruff (1986: 477–478) synonymized this taxon with *Cerion gubernatorium* (Crosse, 1869).

Taxon 112. *Strophiops fulminea* **Maynard and Clapp, 1915 [February 8]: 182** [not illustrated in original publication]; Maynard, 1921b: 149. Examined 1,000 specimens. Measurements not provided.

Type Material. The original description did not distinguish among the 1,000 specimens examined, and there was no mention of type material in the other parts of this publication. Thus, all 1,000 specimens are syntypes. Lot MCZ 76276 was labeled "holotype," but contains three specimens and a label in Maynard's hand containing the term "Type" as well as plate and figure numbers (pl. 45, figs. 9, 10) for illustrations of this taxon that were never published. The specimen that most closely approximates the subsequently published measurements (Maynard, 1921b: 149) is here designated as the lectotype. The remaining two specimens, recatalogued as MCZ 356996, MCZ 76277 (262 specimens), and USNM 420088 (50 specimens), are among the 999 syntypes that become paralectotypes.

Lectotype Measurements. Length 25.2 mm, diameter (excluding lip) 9.7 mm; aperture height (including lip) 9.4 mm, aperture width (including lip and peristome) 8.2 mm.

Type Locality. Very common on rocky shore east of Ft. Winton, New Providence [Island, Bahamas].

Remarks. In the original description, Maynard noted that nearly all were dead in 1913. Later, Maynard (1921b: 149) provided measurements (1.00 by .40 [inches; 25.4 by 10.2 mm]); listed 2,000 specimens, likely by subsequent collection; and referenced illustrations (pl. 45, figs. 5, 6) that were never issued.

Taxon 113. *Strophiops longidentata* Maynard, 1919a [October 16]: 24 [nomen nudum].

Remarks. Not listed in Clench (1957).

Taxon 114. *Strophiops peravita* **Maynard, 1919b [November 6]: 47**; Maynard, 1920d [September 30], pl. 1, figs. 1, 2 [captioned "*S. perantiqua* M. & C."].

Nomenclatural Remarks. The binomen *Strophiops peravita* was used by Maynard (1919b: 47) as a example of a species with a conically tapering shell and was accompanied by a reference to subsequently published figures (Maynard, 1920d, pl. 1, figs. 1, 2) that were captioned "*S. perantiqua* M. & C." Article 10.1.1 (ICZN, 1999: 9) states that if publication of the data relating to a new nominal taxon or a nomenclatural act is interrupted and continued at a later date, the name or act becomes available only when the requirements of the relevant Articles have been met. *Strophiops peravita* became available on November 6, 1919, on the basis of the publication of the meager description, which was adequate to meet the requirements of the relevant article [Article 12.1, ICZN, 1999: 16], rather than from the later publication of the captioned figure. Authorship is attributed to Maynard, the sole author of the description, rather than to Maynard and Clapp, as specified in the caption to the subsequently published illustrations. Ironically, this is the only time that Maynard used the binomen *Strophiops peravita.* It is a lapsus calami because Maynard used the name *Strophiops perantiqua* in two prior references (Maynard, 1919a [October 16]: 15, 1919b [November 6]: 31; in both instances as a nomen nudum) and one subsequent reference (Maynard and Clapp *in* Maynard, 1920d [September 30]: 115, map 1, 2, pl. 1, figs. 1, 2) to this taxon. The figure referred to in the inadvertent description of *S. peravita* is the identical figure referenced in the intended description of this taxon [as *Strophiops perantiqua*], in which

it was noted that it was "contemporary with *S. avita* Mayn."

Type Material. The description of *S. peravita* did not specify the number of specimens examined but included a reference to a subsequently published figure of a single specimen. The 25 specimens mentioned in the intended description of this taxon (as *S. perantiqua* Maynard and Clapp *in* Maynard, 1920d: 115) were available to Maynard in 1919 and are thus part of the type series [Article 72.4.1.1, ICZN, 1999: 76]. *Strophiops peravita* is thus based on 25 syntypes. Lot number MCZ 187537 contains a single specimen that closely matches the illustration mentioned in the taxon description. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of this taxon. The remaining 24 syntypes become paralectotypes.

Lectotype Measurements. Length 31.9 mm, diameter (excluding lip) 14.7 mm; aperture height (including lip) 11.1 mm, aperture width (including lip and peristome) 9.5 mm.

Type Locality. Found fossil in red earth near west coast of Great Guana Key [Exumas, Bahamas], about 1 mile from southern end (see Maynard, 1920d: 117, map 1, location 2 [from the intended taxon description of *Strophiops perantiqua*]). Maynard (1924a: 164) described in detail the locality in which these fossils were collected.

Remarks. Although it seems clear that Maynard intended the taxon to be known as *perantiqua,* it is not possible to consider *peravita* as an "incorrect original spelling" within the confines of Article 32.5.1 (ICZN, 1999: 39) because there is no clear evidence to suggest an alternative spelling within the original publication itself. The name *S. peravita* did not appear in the Batchelder (1951) compilation of Maynard's taxa, nor in Clench's (1957) catalog of *Cerion* taxa. The lectotype of *S. peravita* is also the lectotype of *Strophiops perantiqua* Maynard and Clapp *in* Maynard, 1920, which is a junior objective synonym of *S. peravita* [see Taxon 139, below].

Taxon 115. *Strophiops scalariformis* **Maynard, 1919b [November 6]: 47–48**; Maynard and Clapp *in* Maynard, 1920d [September 30]: 116, map 1, 3, pl. 1, figs. 5, 6 [captioned "*S. scalariformis* M. & C."]. Examined 50 specimens. Size given as 1.20 by .45 [inches; 38.1 by 11.4 mm], but the term "type" was not used.

Nomenclatural Remarks. Maynard (1919b: 48) first used the binomen *Strophiops scalariformis* as a example of a species with a turreted shell and included a reference to subsequently published figures (Maynard, 1920d, pl. 1, figs. 5, 6) that were captioned "*S. scalariformis* M. & C." Article 10.1.1 (ICZN, 1999: 9) states that if publication of the data relating to a new nominal taxon or a nomenclatural act is interrupted and continued at a later date, the name or act becomes available only when the requirements of the relevant Article have been met. *Strophiops scalariformis* became available on November 6, 1919, on the basis of the publication of the meager description, which was adequate to meet the requirements of the relevant articles [Article 12.1, ICZN, 1999: 16],

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Figures 114–125. Taxon 114. *Strophiops peravita* Maynard, 1919. Lectotype MCZ 187537. Fossil in red earth near west coast of Great Guana Key, Exuma Group, Bahamas, about 1 mile from southern end. Taxon 115. *Strophiops scalariformis* Maynard, 1919. Lectotype MCZ 76180. Limited area near beach Great Guana Key, Exuma Group, Bahamas. Taxon 116. *Strophiops inornata* Maynard, 1919. Lectotype MCZ 76049. North side of Bell Key, Exuma Group, Bahamas. Taxon 117. *Strophiops caprana* Maynard, 1919. Lectotype MCZ 76386. North Goat Key off Fresh Creek, Andros, Bahamas. Taxon 118. *Strophiops lobata* Maynard, 1919. Lectotype MCZ 76207. Eastern Soldier Key, Berry Islands, Bahamas. Taxon 119. *Strophiops variata* Maynard and Clapp *in* Maynard, 1919. Lectotype MCZ 76270. Crab Key, Berry Islands, Bahamas. Taxon 120. *Strophiops recessa* Maynard and Clapp *in* Maynard, 1919. Lectotype MCZ 76135. Southern portion of Stocking Island, Exuma Group, Bahamas. Taxon 121.

Strophiops palmata Maynard and Clapp *in* Maynard, 1919. Lectotype MCZ 76179. East and west sides of Wax Key, Exuma Group, Bahamas. Taxon 122. *Strophiops agricola* Maynard and Clapp *in* Maynard, 1919. Lectotype MCZ 76004. Farmer's Key which lies about 1 mile southwest of the southern end of Great Guana Key, Exuma Group, Bahamas. Taxon 123. *Strophiops elegantissima* Maynard, 1919. Lectotype MCZ 76375. Norman's Pond Key, Exuma Group, Bahamas. Taxon 124. *Strophiops arbusta* Maynard and Clapp *in* Maynard, 1919. Lectotype MCZ 76273. Guana Key, Berry Islands, Bahamas. Taxon 125. *Strophiops aspera* Maynard, 1920. Lectotype MCZ 76176. Among dwarf palms in an area about 300 yards long by some 150 wide along the third beach north of south end of Great Guana Key, Exuma Group, Bahamas.

rather than from the later publication of the captioned figure. Authorship is attributed to Maynard, the sole author of the description, rather than to Maynard and Clapp, as specified in the caption to the subsequently published illustrations.

Type Material. The description of *S. scalariformis* did not specify the number of specimens examined, but included a reference to a subsequently published figure of a single specimen. The 50 specimens mentioned in the intended description of this taxon (Maynard and Clapp *in* Maynard, 1920d: 116) were likely available to Maynard in 1919 and are thus part of the type series [Article 72.4.1.1, ICZN, 1999: 76]. *Strophiops scalariformis* is thus based on 50 syntypes. In a subsequent and more detailed description of this taxon, Maynard (1924a: 165) included the statement "dimensions of type .45 by 1.20 [inches; 11.4 by 30.5 mm], aperture .34 [inches; 8.6 mm]." This is regarded as a lectotype designation, and the remaining 49 specimens became paralectotypes. Clench and Aguayo (1952: 430, pl. 56, fig. 2) listed and illustrated MCZ 76180 as the "holotype," presumably on the basis of Maynard's handwritten label using the term "type" that accompanied the specimen. This specimen is the lectotype designated by Maynard.

Lectotype Measurements. Length 30.0 mm, diameter (excluding lip) 11.3 mm; aperture height (including lip) 10.3 mm, aperture width (including lip and peristome) 9.2 mm.

Type Locality. Found in a limited area near beach [Great Guana Key, Exuma Group, Bahamas] (see Maynard, 1920d: 117, map 1, location 3). Maynard (1924a: 165) described in detail the locality in which these fossils were collected.

Remarks. Clench and Aguayo (1952) considered *Cerion scalariforme* to be a synonym of *Cerion asperum* (Maynard and Clapp, 1920).

Taxon 116. *Strophiops inornata* **Maynard, 1919b [November 6]: 49**; Maynard, 1920b [April 8]: 87; Maynard, 1920c [July 10], fig. 73, pl. 17, fig. 2; Maynard, 1920d [September 30]: 112; Maynard and Clapp *in* Maynard, 1920d [September 30]: 126, pl. 3, figs. 11–13. Examined 1,060 specimens. Size given as 1.12 by .45 [inches; 28.4 by 11.4 mm], but the term "type" was not used.

Nomenclatural Remarks. Maynard (1919b: 49) first used the binomen *Strophiops inornata* as a example of a taxon in which the ultimate whorl and aperture are contracted, and included a reference to subsequently published figures (Maynard, 1920d, pl. 3, figs. 11–13) that were captioned "*S. inornata.*" Article 10.1.1 (ICZN, 1999: 9) states that if publication of the data relating to a new nominal taxon or a nomenclatural act is interrupted and continued at a later date, the name or act becomes available only when the requirements of the relevant Articles have been met. *Strophiops inornata* became available on November 6, 1919, on the basis of the publication of the meager description, which was adequate to meet the requirements of the relevant articles [Article 12.1, ICZN, 1999: 16], rather than from the later publication of the captioned figure. Authorship is attributed to Maynard, the sole author of the description.

Before the publication of plate 3, Maynard (1920b [April 8]: 87) again used the name *S. inornata* as an example of morphological reversion following shell damage and cited a figure of a different specimen (Maynard, 1920c [July 10], fig. 73) that was reproduced in color (Maynard, 1920c, pl. 17, fig. 2). In the next issue, Maynard (1920d [September 30]: 112) published a correction stating that figure numbers 72 and 73, as well as plate 17, figures 1 and 2, were transposed and that the figures 73 and plate 17, figure 2, are actually *S. salinaria,* whereas figures 72 and plate 17, figure 1, represent *S. inornata.*

Type Material. The description of *Strophiops inornata* did not specify the num-

ber of specimens examined but included a reference to a subsequently published figure of a single specimen. The 1,060 specimens mentioned in the intended description of this taxon (Maynard and Clapp *in* Maynard, 1920d: 126) were likely available to Maynard in 1919 and are thus part of the type series [Article 72.4.1.1, ICZN, 1999: 76]. *Strophiops inornata* is thus based on 1,060 syntypes. Lot MCZ 76049 was labeled "Holotype" but contained three specimens. Of these, one has an offset final whorl and clearly matches the figures cited in the inadvertent as well as the intended taxon description (Maynard and Clapp *in* Maynard, 1920d [September 30]: 126, pl. 3, figs. 11–13). This specimen is designated to be the lectotype of *Strophiops inornata* Maynard, 1919, to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining two specimens were recatalogued as MCZ 357001 and together with MCZ 76050, MCZ 118190, and USNM 420056, become paralectotypes.

Lectotype Measurements. Length 31.9 mm, diameter (excluding lip) 13.7 mm; aperture height (including lip) 11.6 mm, aperture width (including lip and peristome) 11.0 mm.

Type Locality. North side of Bell Key [Exuma Group, Bahamas].

Taxon 117. *Strophiops caprana* **Maynard, 1919b [November 6]: 52.** *Strophiops capraia* Maynard and Clapp *in* Maynard, 1919c [December 31], fig. 19; Maynard, 1920c, pl. 17, fig. 3; Maynard and Clapp *in* Maynard, 1921a: 131, pl. 28, figs. 7, 8. Examined 1,620 specimens. Size given as 1.12 by .47 [inches; 28.4 by 17.8 mm], but the term "type" was not used.

Nomenclatural Remarks. The binomen *Strophiops caprana* was first used by Maynard (1919b: 52) as an example of a species with a thick margin, and accompanied by a reference to a subsequently published figure (Maynard, 1919c, fig. 19) that was captioned "*S. capraia* M. & C." A colored version of this figure, also labeled *S. capraia,* was published (Maynard, 1920c, pl. 17, fig. 3). Article 10.1.1 (ICZN, 1999: 9) states that if publication of the data relating to a new nominal taxon or a nomenclatural act is interrupted and continued at a later date, the name or act becomes available only when the requirements of the relevant Articles have been met. *Strophiops caprana* became available on November 6, 1919, on the basis of the publication of the meager description, which was adequate to meet the requirements of the relevant articles [Article 12.1, ICZN, 1999: 16], rather than from the later publication of the captioned figure. Authorship is attributed to Maynard, the sole author of the description, rather than to Maynard and Clapp as specified in the caption to the subsequently published illustrations.

Type Material. The description of *Strophiops caprana* did not specify the number of specimens examined but included a reference to a subsequently published figure of a single specimen. The 1,620 specimens mentioned in the intended description of this taxon (Maynard and Clapp *in* Maynard, 1921a: 131) were likely available to Maynard in 1919 and are thus part of the type series [Article 72.4.1.1, ICZN, 1999: 76]. *Strophiops caprana* is thus based on 1,620 syntypes. The specimen illustrated in the originally referenced figure (Maynard, 1919c, fig. 19) could not be identified at the MCZ. Maynard clearly regarded a different specimen to be the "Type" of *Strophiops capraia.* Lot MCZ 76386 was labeled "Holotype" but contains two specimens. One of the specimens approximates the measurements and figures in the intended taxon description and is here selected as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of this taxon. The remaining specimen, recatalogued as MCZ 356997, MCZ 76215, and USNM 420060,

are among the 1,619 syntypes that become paralectotypes.

Lectotype Measurements. Length 28.9 mm, diameter (excluding lip) 12.2 mm; aperture height (including lip) 10.4 mm, aperture width (including lip and peristome) 8.9 mm.

Type Locality. North Goat Key off Fresh Creek [Andros, Bahamas].

Remarks. This taxon has been the victim of multiple lapsus calami, having been spelled *caprana* in the unintended original description (Maynard, 1919b: 52), *capraia* in text and figure captions (Maynard, 1919c, fig. 19, 1920b: 81, 1920c, pl. 17, fig. 3) and in the intended taxon description (Maynard and Clapp *in* Maynard, 1921a: 131, pl. 28, figs. 7, 8), and *capria* (Maynard, 1924b?: [3]) in the sales catalog. Although it seems clear that Maynard intended the taxon to be known as *capraia*, it is not possible to consider *caprana* as an "incorrect original spelling" within the confines of Article 32.5.1 (ICZN, 1999: 39) because there is no clear evidence to suggest an alternative spelling within the original publication itself. This taxon was also listed as *S. capraia* by Clench (1957: 139).

Taxon 118. *Strophiops lobata* **Maynard, 1919b [November 6]: 52**; Maynard and Clapp *in* Maynard, 1919c [December 31], fig. 20; Maynard, 1920b: 81; Maynard, 1920c, fig. 64, pl. 14, fig. 4; Maynard and Clapp *in* Maynard, 1921a: 134, pl. 31 [erroneously listed as pl. 30], figs. 7, 8. Examined 925 specimens. Size given as 1.11 by .45 [inches; 30.5 by 11.4 mm], but the term "type" was not used.

Nomenclatural Remarks. The binomen *Strophiops lobata* was used by Maynard (1919b: 527) as an example of a species with a thickened and lobed margin and included a reference to a subsequently published figure (Maynard, 1919c, fig. 20) that was labeled "*S. lobata* M. & C." Article 10.1.1 (ICZN, 1999: 9) states that if publication of the data relating to a new nominal taxon or a nomenclatural act is interrupted and continued at a later date, the name or act becomes available only when the requirements of the relevant Articles have been met. *Strophiops lobata* became available on November 6, 1919, on the basis of the publication of the meager description, which was adequate to meet the requirements of the relevant articles [Article 12.1, ICZN, 1999: 16], rather than from the later publication of the captioned figure. Authorship is attributed to Maynard, the sole author of the description, rather than to Maynard and Clapp, as specified in the caption to the subsequently published illustrations.

Type Material. The unintended taxon description of *Strophiops lobata* did not specify the number of specimens examined but included a reference to a subsequently published figure of a single specimen. The 925 specimens mentioned in the intended description of this taxon (Maynard and Clapp *in* Maynard, 1921a: 134) were likely available to Maynard in 1919 and are thus part of the type series [Article 72.4.1.1, ICZN, 1999: 76]. *Strophiops lobata* is thus based on 925 syntypes. The specimen illustrated in figure 20 could not be identified at the MCZ. Maynard clearly regarded a different specimen to be the "Type" of *Strophiops lobata.* Lot MCZ 76207 contains a single specimen labeled "Holotype" that approximates the illustration and the measurements of this taxon in the intended taxon description and is accompanied by a label in Maynard's hand with the term "type," which includes references to these figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining specimens, including MCZ 76208 and USNM 420147, are paralectotypes.

Lectotype Measurements. Length 29.1 mm, diameter (excluding lip) 11.9 mm; aperture height (including lip) 11.4 mm, aperture width (including lip and peristome) 8.9 mm.

Type Locality. Eastern Soldier Key, Berry Islands, Bahamas.

Remarks. Maynard (1920b: 81) again used the name *S. lobata* prior to the intended description of the taxon, referencing a subsequently published figure (Maynard, 1920c, fig. 64) that was identical to figure 20 but captioned "*S. caduca* M. & C." A colored version of figures 20 and 64 (Maynard, 1920c, pl. 14, fig. 4) is captioned "*S. caduca.*" Maynard (1920d: 112) published corrections, stating that the captions to figures 64 and pl. 14, fig. 4, should read *lobata* not *caduca.*

Taxon 119. *Strophiops variata* **Maynard and Clapp *in* Maynard, 1919c [December 31]: 55, figs. 27, 28**; Maynard, 1920a: 77, 78, fig. 54; Maynard, 1920c, pl. 14, fig. 5; Maynard and Clapp *in* Maynard, 1921a: 134, pl. 32, figs. 1, 2. Examined 1,132 specimens. Measurements not provided.

Nomenclatural Remarks. The binomen *Strophiops variata* was used by Maynard (1919c: 55, figs. 27, 28) as an example of a taxon with margins malformed after incorporation of a limestone granule in the peristome and accompanied by figures of three specimens labeled "*S. variata* M. & C." The association of a new species group name with an illustration of the taxon being named before 1931 makes the name *Strophiops variata* Maynard and Clapp *in* Maynard, 1919c [December 31]: 55, figs. 27, 28, available (Article 12.2.7, ICZN, 1999: 17) prior to the intended description of this species (Maynard and Clapp *in* Maynard, 1921a [May 2]: 134, pl. 32, figs. 1, 2).

Type Material. Maynard's (1919c: 55–56) first use of the name *S. variata* was as an example of a deformation that could occur in some specimens after incorporation of a limestone granule in the peristome. He mentioned that this produced a protuberance in a total of six specimens of *S. variata* and illustrated portions of three of the malformed specimens. It is likely that the six deformed specimens were selected from among the 1,132 specimens mentioned in the intended description of this taxon (Maynard and Clapp *in* Maynard, 1921a: 134) that were available to him at the time. All 1,132 specimens are thus part of the type series [Article 72.4.1.1, ICZN, 1999: 76], and *Strophiops lobata* is based on 1,132 syntypes. None of the figured specimens could be identified at the MCZ. Maynard clearly regarded a different specimen to be the "Type" of *Strophiops variata.* Lot MCZ 76270 contained two specimens in a lot labeled "Holotype," one smooth, with weak costae limited to the final whorl, the other with strong costae over the entire shell. The smooth specimen, which more closely agrees with the intended taxon description and figures, is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The strongly costate specimen was recatalogued as MCZ 356998. It and the remaining specimens, including MCZ 76271, MCZ 118258, and USNM 420123, are paralectotypes.

Lectotype Measurements. Length 31.3 mm, diameter (excluding lip) 10.7 mm; aperture height (including lip) 10.7 mm, aperture width (including lip and peristome) 8.8 mm.

Type Locality. Crab Key, Berry Islands, Bahamas.

Remarks. Other uses of the binomen prior to its intended original description include Maynard (1920a: 77, 78, fig. 54, 1920c, caption to pl. 14, fig. 5).

Taxon 120. *Strophiops recessa* **Maynard and Clapp *in* Maynard, 1919c [December 31]: 57, figs. 29A, B**; Maynard, 1920c, pl. 17, fig. 6; Maynard and Clapp *in* Maynard, 1920d: 122, pl. 24, figs. 2, 3. Examined 1,147 specimens. Size given as 1.15 by .45 [inches; 29.2 by 11.4 mm], but the term "type" was not used.

Nomenclatural Remarks. Maynard (1919c: 57, figs. 29A, B) first used the bi-

nomen *Strophiops recessa* as an example of a species that has an enlarged, ear-like frontal bar encroaching on the umbilicus and included illustrations (figs. 29A, B) captioned "*S. recessa* M. & C." The association of a new species group name with an illustration of the taxon being named before 1931 makes the name *Strophiops recessa* Maynard and Clapp *in* Maynard, 1919c (p. 57, figs. 29A, B), available on December 31, 1919 (Article 12.2.7, ICZN, 1999: 17), prior to the intended description of this species (Maynard and Clapp *in* Maynard, 1920d: 122, pl. 24, figs. 2, 3).

Type Material. The description of *Strophiops recessa* did not specify the number of specimens examined but included figures of a single specimen. The 1,147 specimens mentioned in the intended description of this taxon (Maynard and Clapp *in* Maynard, 1920d: 122) were likely available to Maynard at the time and are thus part of the type series [Article 72.4.1.1, ICZN, 1999: 76]. *Strophiops recessa* is based on 1,147 syntypes.

The originally illustrated specimen (Maynard, 1919c, figs. 29A, B) could not be identified at the MCZ. Maynard clearly regarded a different specimen to be the "Type" of *Strophiops recessa.* Lot MCZ 76135 contained a single specimen labeled "Holotype" that approximates the measurements and illustration of this taxon in the intended description (Maynard and Clapp *in* Maynard, 1920d: 122, pl. 24, figs. 2, 3) and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen (MCZ 76135) is here designated as the lectotype of *Strophiops recessa* Maynard and Clapp *in* Maynard, 1919, to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining specimens, including MCZ 76136, MCZ 118346, and USNM 420106, are paralectotypes.

Lectotype Measurements. Length 29.9 mm, diameter (excluding lip) 11.3 mm; aperture height (including lip) 10.3 mm, aperture width (including lip and peristome) 8.1 mm.

Type Locality. Southern portion of Stocking Island, Exuma Cays, Bahamas.

Remarks. It is not surprising that, after Maynard's death, the specimens labeled as "types" by Maynard were the ones to be segregated at the MCZ, while the many remaining specimens were dispersed among MCZ, USNM, and other institutions (Turner, 1957: 151). Given the quality of Maynard's illustrations, it is unlikely that the initially illustrated specimen could ever be discerned unambiguously from among the large number of remaining specimens, even if it were present among them.

Taxon 121. *Strophiops palmata* **Maynard and Clapp *in* Maynard, 1919c [December 31]: 59–60, 64, figs. 32, 32*, 33, 34A–D, 35, [35]B, pl. 10, figs. 1, 2, 8**; Maynard, 1920a: 76, 77; Maynard, 1920b, fig. 58, pl. 12, fig. 2; Maynard, 1920c: 86, fig. 67, pl. 14, fig. 2, fig. 71, pl. 16, figs. 4, 5; Maynard and Clapp *in* Maynard, 1920d: 120, pl. 21, figs. 6, 7; Maynard, 1926: 203–212. Examined 3,422 specimens. Size given as 1.25 by .45 [inches; 31.8 by 11.4 mm], but the term "type" was not used.

Nomenclatural Remarks. The binomen *Strophiops palmata* was first used by Maynard (1919c: 59–60, 64, figs. 32, 32*, 33, 34A–D, 35, [35]B, pl. 10, figs. 1, 2, 8) to illustrate pathological duplication and/or migration of teeth within the shell aperture after shell damage. Portions of at least six different specimens are illustrated in these figures, of which figures 32, 32*, and 33 and pl. 10, figs. 1, 2, and 8, are captioned "*S. palmata* M & C.," whereas figures 34A–D, 35, and 35B are captioned "*S. palmata.*" The association of a new species group name with an illustration of the taxon being named before 1931 makes the name *Strophiops palmata* Maynard and Clapp *in* Maynard 1919c (pp. 59–60, 64, figs. 32, 32*, 33, 34A–D, 35, [35]B, pl.

10, figs. 1, 2, 8), available (Article 12.2.7, ICZN, 1999: 17) prior to the intended description of this species (Maynard and Clapp *in* Maynard, 1920d: 120, pl. 21, figs. 6, 7).

Maynard (1920a: 76, 77) again used *S. palmata* as an example of a taxon that agglutinates sand, citing a subsequently published illustration of another specimen (Maynard, 1920b, fig. 58, pl. 12, fig. 2). Additional damaged specimens are illustrated (Maynard, 1920c: 86, fig. 67, repeated on pl. 14, fig. 2, fig. 71, repeated on pl. 16, figs. 4, 5). All of these uses of the name preceded the intended original description of *Strophiops palmata.*

Type Material. The description of *Strophiops palmata* did not specify the number of specimens examined, but included figures of portions of six specimens. The 3,422 specimens mentioned in the intended description of this taxon (Maynard and Clapp *in* Maynard, 1920d: 120) were likely available to Maynard at the time, and are thus part of the type series [Article 72.4.1.1, ICZN, 1999: 76]. *Strophiops recessa* is based on 3,422 syntypes. None of the six initially figured specimens could be identified at the MCZ. Maynard clearly regarded a different specimen to be the "Type" of *Strophiops palmata.* Lot MCZ 76179 contains a single specimen labeled "Holotype" that approximates the measurements and illustration of this taxon in the intended description (Maynard and Clapp *in* Maynard, 1920d: 122, pl. 24, figs. 2, 3) and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen (MCZ 76179) is here designated as the lectotype of *Strophiops palmata* Maynard and Clapp *in* Maynard, 1919, to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 3,415 specimens, including MCZ 76178, MCZ 118352, and USNM 420024, are paralectotypes.

Lectotype Measurements. Length 27.6 mm, diameter (excluding lip) 11.0 mm; aperture height (including lip) 10.3 mm, aperture width (including lip and peristome) 7.7 mm.

Type Locality. East and west sides of Wax Key [Exuma Group, Bahamas].

Remarks. It is not surprising that, following Maynard's death, the specimens labeled as "types" by Maynard were the ones to be segregated at the MCZ, while the many remaining specimens were dispersed among MCZ, USNM, and other institutions (Turner, 1957: 151). The anomalies in dentition make the six illustrated specimens distinctive, yet they were not found in the collections of either MCZ or USNM. Maynard (1920d: 120) reported this taxon to be very abundant on palm fronds and under them. Maynard (1926: 203–212) provided additional, detailed information on the animals and anatomy, noting that 2,683 specimens were collected in 2 or 3 hours.

Taxon 122. *Strophiops agricola* **Maynard and Clapp *in* Maynard, 1919c [December 31]: 64, figs. 35C, D**; Maynard, 1920d, pl. 22, figs. 6, 7; Maynard, 1924c: 1. Examined 80 specimens. Size given as 1.15 by .40 [inches; 29.2 by 10.2 mm], but the term "type" was not used.

Nomenclatural Remarks. The first use of the binomen *Strophiops agricola* appeared in a discussion of the occasional appearance of a tooth-like concretion along the shell margin (Maynard, 1919c, figs. 35C, D, p. 64). The caption to the figures, which illustrate the malformed aperture of a specimen (fig. 35C) as well as an enlargement of the concretion (fig. 35D), reads "*S. agricola* M & C.," establishing the authorship of the taxon as Maynard and Clapp *in* Maynard. The association of a new species group name with an illustration of the taxon being named before 1931 makes the name *Strophiops agricola* Maynard and Clapp *in* Maynard, 1919c (figs. 35C, D), available (Article 12.2.7, ICZN, 1999: 17) prior to the intended description of this species (Maynard, 1924c: 1). The

name was next used in the caption to illustrations (Maynard, 1920d, pl. 22, figs. 6, 7) published 4 years before the intended description.

Type Material. Only a single specimen was referred to in the inadvertent description of *Strophiops agricola.* The intended taxon description (Maynard, 1924c: 1) mentioned 80 specimens. It is likely that at least some if not all of these were available to Maynard in 1919. *Strophiops agricola* is thus based on ≤80 syntypes.

Neither of the figures on which the taxon is based shows an entire specimen; rather, they provide details of a concretion on a portion of the outer lip. An examination of the 49 specimens in MCZ 76004 that were labeled "paratypes" uncovered the originally illustrated specimen (Maynard, 1919c, fig. 35). This specimen is here designated as the lectotype. The remaining specimens were recatalogued as MCZ 356999 and together with MCZ 76003 and MCZ 118252 are among the ≤79 specimens that become paralectotypes.

Lectotype Measurements. Length 28.0 mm, diameter (excluding lip) 10.7 mm; aperture height (including lip) 9.1 mm, aperture width (including lip and peristome) 7.5 mm.

Type Locality. Farmer's Key which lies about 1 mile southwest of the southern end of Great Guana Key, Exuma Group, Bahamas.

Remarks. Maynard clearly regarded a different specimen to be the "Type" of *Strophiops agricola.* Lot MCZ 76003 contains a single specimen labeled "Holotype" that approximates the subsequent illustrations (Maynard, 1920d, pl. 22, figs. 6, 7) and the measurements in the intended description (Maynard, 1924c: 1). This specimen, a paralectotype, is accompanied by a label in Maynard's hand with the term "type," which includes references to the previously published plates.

Taxon 123. *Strophiops elegantissima* **Maynard, 1919c [December 31]: 64, figs. 36A–D**; Maynard, 1920a: 80; Maynard, 1920b, fig. 60, pl. 13, fig. 2; *Multistrophia elegantissima* Maynard and Clapp *in* Maynard, 1920d: 126, pl. 25, figs. 1, 2. Unspecified number of specimens examined. Size given as 1.25 by .50 [inches; 31.8 by 12.7 mm], but the term "type" was not used.

Nomenclatural Remarks. The binomen *Strophiops elegantissima* was first published by Maynard (1919c: 64, figs. 36A–D) together with illustrations labeled "*S. elegantissima.*" The text provided detailed descriptions of dentition stated to be a specific character in *S. elegantissima.* The name *Strophia elegantissima* Maynard becomes available on December 31, 1919 (Articles 12.1 and 12.2.7, ICZN, 1999: 17), prior to the intended description of the taxon as *Multicostata elegantissima* Maynard and Clapp *in* Maynard, 1920d (p. 126, pl. 25, figs. 1, 2). Because figures 36A–D are captioned "*S. elegantissima,*" the taxon must be attributed to Maynard rather than to Maynard and Clapp, as cited by Clench (1957: 144). The name *S. elegantissima* was again used by Maynard (1920a: 80) as an example of a taxon with color banding, citing a subsequently published illustration (Maynard, 1920b, fig. 60, identical image colored on pl. 13, fig. 2, both captioned "*S. elegantissima* M. & C.").

Type Material. The description of *Strophiops elegantissima* did not specify the number of specimens examined but included figures of portions of a single specimen. The number of specimens examined was not specified in the intended description of this taxon (Maynard and Clapp *in* Maynard, 1920d: 126). Although these were likely available to Maynard in 1919 and are part of the type series [Article 72.4.1.1, ICZN, 1999: 76], the number of syntypes is unclear. The initially illustrated specimen could not be located at the MCZ. Maynard clearly regarded a different specimen to be the "Type" of *Strophiops elegantissima.* Lot MCZ 76375 contains a single specimen labeled "Ho-

lotype" that approximates the measurements and illustration of this taxon in the intended description (Maynard and Clapp *in* Maynard, 1920d: 126, pl. 25, figs. 1, 2) and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen (MCZ 76375) is here designated as the lectotype of *Strophiops elegantissima* Maynard, 1919, to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining specimens, including MCZ 76183, MCZ 118239, and USNM 420105, are paratypes.

Lectotype Measurements. Length 32.3 mm, diameter (excluding lip) 11.1 mm; aperture height (including lip) 10.8 mm, aperture width (including lip and peristome) 8.7 mm.

Type Locality. Norman's Pond Key [Exuma Group, Bahamas].

Remarks. It is not surprising that after Maynard's death the specimens labeled as "types" by Maynard were the ones to be segregated at the MCZ while the many remaining specimens were dispersed among MCZ, USNM, and other institutions (Turner, 1957: 151). Although Maynard's illustrations (Maynard, 1919c, figs. 36A–D, 1920b, fig. 60, pl. 13, fig. 2, 1920d: 126, pl. 25, figs. 1, 2) are of sufficient quality to conclude that the shells figured are different specimens, we have not been able to match the earliest figure with any of the specimens available to us.

Taxon 124. *Strophiops arbusta* **Maynard and Clapp *in* Maynard, 1919c [December 31]: 65, fig. 38**; Maynard, 1920a: 74, fig. 49; Maynard and Clapp *in* Maynard, 1921a: 133, pl. 30, figs. 5, 6. Examined 2,454 specimens. Size given as 1.24 by .48 [inches; 30.5 by 11.4 mm], but the term "type" was not used.

Nomenclatural Remarks. The binomen *Strophiops arbusta* was first published by Maynard (1919c: 65, fig. 38) as an example of a species that lacked an upper [columellar] tooth. The figure was captioned "*S. arbusta* M. & C." This illustration was later reproduced in color (Maynard, 1920c, pl. 16, fig. 6). The association of a new species group name with an illustration of the taxon being named before 1931 makes the name *Strophiops arbusta* Maynard and Clapp *in* Maynard (1919c: 65, fig. 38) available (Article 12.2.7, ICZN, 1999: 17) prior to the intended description of this species (Maynard and Clapp *in* Maynard, 1921a: 133, pl. 30, figs. 5, 6). Maynard (1920a: 74, figs. 49A, B) again used the name in conjunction with figures before the intended introduction of the taxon. These illustrations were later reproduced in color (Maynard, 1920b, pl. 12, figs. 4, 5).

Type Material. The description of *Strophiops arbusta* did not specify the number of specimens examined but included a figure of a single specimen. The 2,454 specimens mentioned in the intended description of this taxon (Maynard and Clapp *in* Maynard, 1921a: 133) were likely available to Maynard at the time and are thus part of the type series [Article 72.4.1.1, ICZN, 1999: 76]. *Strophiops arbusta* is based on 2,454 syntypes. The originally illustrated specimen (Maynard, 1919c, fig. 38) could not be identified at the MCZ. Maynard clearly regarded a different specimen to be the "Type" of *Strophiops arbusta.* Lot MCZ 76273 contains a single specimen labeled "Holotype" that approximates the illustration more than the measurements of this taxon and is accompanied by a label in Maynard's hand with the term "Holotype" added later. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining specimens, including MCZ 76272, USNM 419968, and USNM 420027, are paralectotypes.

Lectotype Measurements. Length 29.8 mm, diameter (excluding lip) 11.0 mm; aperture height (including lip) 10.4 mm, ap-

erture width (including lip and peristome) 8.6 mm.

Type Locality. Guana Key, Berry Islands, Bahamas.

Remarks. It is not surprising that, after Maynard's death, the specimens labeled as "types" by Maynard were the ones to be segregated at the MCZ, while the many remaining specimens were dispersed among MCZ, USNM, and other institutions (Turner, 1957: 151). Given the quality of Maynard's illustrations, it is unlikely that the initially figured specimen could ever be discerned unambiguously from among the large number of remaining specimens, even if it were present among them.

Taxon 125. *Strophiops aspera* Maynard, 1919a [October 16]: 14 [nomen nudum]; **Maynard, 1920a [February 29]: 77**; Maynard and Clapp *in* Maynard, 1920b [April 8]: 89, fig. 57, pl. 12, fig. 1; Maynard and Clapp *in* Maynard, 1920d: 116; maps 1, 4, pl. 1, figs. 9, 10. Examined 1,500 specimens. Size given as 1.06 by .30 [inches; 26.9 by 7.6 mm], but the term "type" was not used.

Nomenclatural Remarks. Maynard (1919a: 14) first introduced the binomen *Strophiops aspera* as a nomen nudum. He again (Maynard, 1920a: 77) used this taxon name as an example of a species in which the animal gathered grains of carbonate sand and fastened them to outer and inner surfaces of the shell, citing a subsequently published illustration (Maynard, 1920b, fig. 57) captioned "*S. aspera* M & C." Article 10.1.1 (ICZN, 1999: 9) states that if publication of the data relating to a new nominal taxon or a nomenclatural act is interrupted and continued at a later date, the name or act becomes available only when the requirements of the relevant Articles have been met. *Strophiops aspera* became available on February 29, 1920, on the basis of the publication of the description, which was adequate to meet the requirements of the relevant articles [Article 12.1, ICZN, 1999: 16], rather than from the later publication of the captioned figure. Authorship is attributed to Maynard, the sole author of the description.

Type Material. The description of *S. aspera* did not specify the number of specimens examined, but included a reference to a subsequently published figure of a single specimen. The 1,500 specimens mentioned in the intended description of this taxon (Maynard and Clapp *in* Maynard, 1920d: 116) were likely available to Maynard at the time he wrote the unintended species description and are thus part of the type series [Article 72.4.1.1, ICZN, 1999: 76]. *Strophiops aspera* is therefore based on 1,500 syntypes. The figured specimen (Maynard, 1920b, fig. 57) could not be recognized at the MCZ. Maynard clearly regarded a different specimen to be the "Type" of *Strophiops aspera.* Lot MCZ 76176 contains a single specimen labeled "Holotype" that, at best, approximates the measurements and illustrations of this taxon in the intended description. This specimen is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures on plate 1. Clench and Aguayo (1952: 430, pl. 56, fig. 1) illustrated this specimen as the "Holotype" of *Cerion asperum.* Article 74.5 (ICZN, 1999: 82) states, "When the original work reveals that the taxon had been based on more than one specimen, a subsequent use of the term 'holotype' does not constitute a valid lectotype designation unless the author, when wrongly using that term, explicitly indicated that he or she was selecting from the type series that particular specimen to serve as the name-bearing type." Thus, Clench and Aguayo's treatment of MCZ 76176 can not be considered a lectotype designation. This specimen (MCZ 76176) is here designated as the lectotype of *Strophiops aspera* Maynard, 1920, to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original, and Clench and Aguayo's subse-

quent, concepts of it. The remaining specimens are paralectotypes.

Lectotype Measurements. Length 24.8 mm, diameter (excluding lip) 9.6 mm; aperture height (including lip) 7.6 mm, aperture width (including lip and peristome) 7.0 mm.

Type Locality. Among dwarf palms in an area about 300 yards long by some 150 wide along the third beach N of the S end of [Great Guana] key [Exuma Group, Bahamas].

Remarks. It is not surprising that, after Maynard's death, the specimens labeled as "types" by Maynard were the ones to be segregated at the MCZ, while the many remaining specimens were dispersed among MCZ, USNM, and other institutions (Turner, 1957: 151). Given the quality of Maynard's illustrations of this species, it is unlikely that the initially figured specimen, shown only in right lateral view, could ever be discerned unambiguously from among the large number of specimens. Maynard (1920d: 116) reported this taxon to be abundant, but mostly dead. Out of 1,500 specimens collected, only 70 were living. Maynard (1924a: 167) contradicted this number, stating that of 953 collected, 70 were living, and provided more detailed descriptions of the shell, ecology, and anatomy of this taxon. Clench and Aguayo (1952) considered *Cerion asperum* to be a valid species and the senior synonym of *Strophiops scalariformis.*

Taxon 126. *Strophiops fruticosa* Maynard, 1920a [February 29]: 77 [nomen nudum]; **Maynard and Clapp *in* Maynard, 1920b [April 8], fig. 55, pl. 12, fig. 3**; Maynard and Clapp *in* Maynard, 1920d: 125, pl. 20, figs. 3, 4. Examined 1,040 specimens. Size given as 1.25 by .45 [inches; 31.8 by 11.4 mm], but the term "type" was not used.

Nomenclatural Remarks. Maynard (1920a: 77) first introduced the binomen *Strophiops fruticosa* as one of two examples of a taxon that occasionally has depressions in their surface sculpture but noted explicitly that this was not a specific character. This use was a nomen nudum, but included a reference to a subsequently published illustration (Maynard, 1920b, fig. 55, identical illustration colored on pl. 12, fig. 3, both captioned "*S. fruticosa* M. & C."). The association of a new species group name with an illustration of the taxon being named prior to 1931 makes the name *Strophiops fruticosa* Maynard and Clapp *in* Maynard, 1920b (fig. 55, pl. 12, fig. 3), available (Article 12.2.7, ICZN, 1999: 17) prior to the intended description of this species (Maynard and Clapp *in* Maynard, 1920d: 125, pl. 20, figs. 3, 4).

Type Material. Although the unintended description of *Strophiops fruticosa* makes reference only to a single specimen shown in figure 55, it is likely that the 1,040 specimens mentioned in the intended description of this taxon (Maynard and Clapp *in* Maynard, 1920d: 125) were available to Maynard at the time and are thus part of the type series [Article 72.4.1.1, ICZN, 1999: 76]. *Strophiops fruticosa* is based on 1,040 syntypes.

The specimen illustrated in Maynard (1920b, fig. 55, pl. 12, fig. 3) could not be located at the MCZ. Maynard clearly regarded a different specimen to be the "Type" of *Strophiops fruticosa.* Lot MCZ 76239 contains a single specimen labeled "Holotype" that approximates the measurements and illustration of this taxon in the intended description (Maynard and Clapp *in* Maynard, 1920d: 125, pl. 20, figs. 3, 4) and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen (MCZ 76239) is here designated as the lectotype of *Strophiops fruticosa* Maynard, 1920, to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining specimens, including MCZ 76240, MCZ 118290, and USNM 420099, are paralectotypes.

Lectotype Measurements. Length 29.3

mm, diameter (excluding lip) 11.5 mm; aperture height (including lip) 10.5 mm, aperture width (including lip and peristome) 8.8 mm.

Type Locality. Bush Key [Exuma Group, Bahamas].

Remarks. It is not surprising that, following Maynard's death, the specimens labeled as "types" by Maynard were the ones to be segregated at the MCZ, while the many remaining specimens were dispersed among MCZ, USNM, and other institutions (Turner, 1957: 151). Given the quality of Maynard's illustration of a dorsal view of the single shell, it is unlikely that this specimen could ever be discerned unambiguously from among the large number of remaining specimens, even if it were present among them.

Maynard (1920d: 125) reported this taxon to be common on the ground or about the bases of bushes.

Taxon 127. *Strophiops caduca* Maynard, 1919b [November 6]: 35 [nomen nudum]; Maynard, 1920a [February 29]: 77 [nomen nudum]; **Maynard and Clapp *in* Maynard, 1920b [April 8], fig. 56,** 82; Maynard, 1920c, figs. 61A, 64, pl. 14, fig. 4 [see Nomenclatural Remarks], pl. 15, fig. 4; Maynard and Clapp *in* Maynard, 1921a: 133, pl. 30, figs. 9, 10. Examined 1,278 specimens. Size given as 1.00 by .45 [inches; 25.4 by 11.4 mm], but the term "type" was not used.

Nomenclatural Remarks. The binomen *Strophiops caduca* first appeared as a nomen nudum (Maynard, 1919b: 35). Maynard (1920a: 77) again used this binomen as one of two examples of a taxon that occasionally had depressions in its surface sculpture, but noted explicitly that this was not a specific character. This use, also a nomen nudum, included a reference to a subsequently published illustration (Maynard, 1920b, fig. 56, captioned "*S. caduca* M. & C."). The association of a new species group name with an illustration of the taxon being named before 1931 makes the name *Strophiops caduca* Maynard and Clapp *in* Maynard, 1920b (fig. 56), available (Article 12.2.7, ICZN, 1999: 17) prior to the intended description of this species (Maynard and Clapp *in* Maynard, 1921a: 133, pl. 30, figs. 9, 10). Maynard (1920b: 82) again used the binomen citing figures (Maynard, 1920c, fig. 61A) of a different specimen, captioned "*S. caduca.*" The binomen "*S. caduca* M. & C." appears in the caption to figure 64 (Maynard, 1920c), which is identical to figure 20 (Maynard, 1919c), captioned "*S. lobata* M. & C." A colored version of figures 20 and 64 (Maynard, 1920c, pl. 14, fig. 4) is captioned "*S. caduca.*" Maynard (1920d: 112) published corrections, stating that the captions to figures 64 and pl. 14, fig. 4, should read *lobata* not *caduca.*

Type Material. Although the unintended description of *Strophiops caduca* makes reference only to a single specimen shown in figure 56, it is likely that the 1,278 specimens mentioned in the intended description of this taxon (Maynard and Clapp *in* Maynard, 1921a: 133) were available to Maynard at the time, and are thus part of the type series [Article 72.4.1.1, ICZN, 1999: 76]. *Strophiops caduca* is based on 1,278 syntypes.

The specimen illustrated in Maynard, 1920b (fig. 56), could not be identified at

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Figures 126–137. Taxon 126. *Strophiops fruticosa* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76239. Bush Key, Exuma Group, Bahamas. Taxon 127. *Strophiops caduca* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76366. West side of Cabbage Key, Berry Islands, Bahamas. Taxon 128. *Strophiops persuasa* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76189. Along shore north of Fresh Creek, Andros, Bahamas. Taxon 129. *Strophiops santesoni* Maynard, 1920. Lectotype MCZ 358073. Along northern shore of New Providence Island, west of Nassau from second mile post to beyond the fourth. Taxon 130. *Strophiops inconstans* Maynard, 1920. Lectotype MCZ 76341. West side of Bird Key, Exuma Group, Bahamas. Taxon 131. *Strophiops plebeia* Maynard, 1920. Lectotype USNM 420125. Lignumvitae Key, Berry Islands, Bahamas. Taxon 132.

Strophiops cana Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76374. Fortune Key, Berry Islands, Bahamas. Taxon 133. *Strophiops territa* Maynard, 1920. Lectotype MCZ 76396. Methodist churchyard and vicinity, Sherley Street, Nassau, New Providence Island, Bahamas. Taxon 134. *Strophiops albolabra* Maynard, 1920. Lectotype MCZ 76255. Great Harbor Key, Berry Islands, Bahamas. Taxon 135. *Strophiops fragilis* Maynard, 1920. Lectotype MCZ 76166. Second westernmost Brigadier Key, Great Exuma, Exuma Group, Bahamas. Taxon 136. *Strophiops latonia* Maynard, 1920. Lectotype MCZ 76314. St. Paul's Quarry off West Sherley St., Nassau, New Providence Island, Bahamas. Taxon 137. *Strophiops mariae* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76204. Maria Key near Little Exuma, Exuma Group, Bahamas.

the MCZ. Maynard clearly regarded a different specimen to be the "Type" of *Strophiops caduca.* Lot MCZ 76366 contains a single specimen labeled "Holotype" that approximates the illustration more than the measurements of this taxon in the intended taxonomic description (Maynard and Clapp *in* Maynard, 1921a: 133, pl. 30, figs. 9, 10) and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures on plate 30. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. Maynard's remaining specimens, including MCZ 76365 and USNM 420005, are paralectotypes.

Lectotype Measurements. Length 27.4 mm, diameter (excluding lip) 11.8 mm; aperture height (including lip) 10.3 mm, aperture width (including lip and peristome) 8.7 mm.

Type Locality. West side of Cabbage Key [Berry Islands], Bahamas.

Remarks. It is not surprising that, after Maynard's death, the specimens labeled as "types" by Maynard were the ones to be segregated at the MCZ, while the many remaining specimens were dispersed among MCZ, USNM, and other institutions (Turner, 1957: 151). Given the quality of Maynard's illustrations of the dorsal view of the shell, it is unlikely that this specimen could ever be discerned unambiguously from among the large number of remaining specimens, even if it were present among them.

Taxon 128. *Strophiops persuasa* **Maynard and Clapp *in* Maynard, 1920b [April 8], fig. 59*, pl. 13, fig. 1**; Maynard, 1920d: 112; Maynard and Clapp *in* Maynard, 1921a: 131, pl. 28, figs. 9, 10. Examined 2,428 specimens. Size given as .98 by .40 [inches; 24.9 by 10.2 mm], but the term "type" was not used.

Nomenclatural Remarks. This taxon became available when an illustration (Maynard, 1920b, fig. 59*, pl. 13, fig. 1) captioned "*S. persuasa* M. & C." was published. The association of a new species group name with an illustration of the taxon being named before 1931 makes the name *Strophiops persuasa* Maynard and Clapp *in* Maynard, 1920, available (Article 12.2.7, ICZN, 1999: 17) prior to the intended description of this species (Maynard and Clapp *in* Maynard, 1921a: 131, pl. 28, figs. 7, 8). The name next appeared (Maynard, 1920d: 112) in a text correction [see nomenclatural remarks under *S. santesoni,* Taxon 129].

Type Material. Although the unintended description of *Strophiops persuasa* makes reference only to a single specimen illustrated in figure 59*, it is likely that the 2,428 specimens mentioned in the intended description of this taxon (Maynard and Clapp *in* Maynard, 1921a: 131) were available to Maynard at the time and are thus part of the type series [Article 72.4.1.1, ICZN, 1999: 76]. *Strophiops persuasa* is based on 2,428 syntypes. The specimen figured both in figure 59* and on plate 13, figure 1, could not be located at the MCZ. Maynard clearly regarded a different specimen to be the "Type" of *Strophiops persuasa.* Lot MCZ 76189 was labeled "Holotype" but contained two specimens. The larger of these specimens approximates the subsequently published measurements and figures and is here selected as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of this taxon. The remaining specimen was recatalogued as MCZ 357000 and, together with MCZ 76188 and USNM 420124, are among the 2,427 specimens that become paralectotypes.

Lectotype Measurements. Length 25.8 mm, diameter (excluding lip) 10.8 mm; aperture height (including lip) 8.9 mm, aperture width (including lip and peristome) 7.9 mm.

Type Locality. Along shore north of Fresh Creek, Andros, Bahamas.

Remarks. It is not surprising that, after

Maynard's death, the specimens labeled as "types" by Maynard were the ones to be segregated at the MCZ, while the many remaining specimens were dispersed among MCZ, USNM, and other institutions (Turner, 1957: 151). Given the quality of Maynard's illustration of an apertural view, it is unlikely that this specimen could ever be discerned unambiguously from among the large number of specimens, even if it were present among them.

Taxon 129. *Strophiops santesoni* Maynard, 1920a [February 29]: 80, 81 [nomen nudum]; Maynard, 1920b [April 8], fig. 59; **Maynard, 1920c [July 10], fig. 62, pl. 15, fig. 5 [both of sinistral specimen]**; Maynard and Clapp *in* Maynard, 1921b: 139, pl. 36, figs. 3, 4, pl. 15, fig. 5. Examined 1,964 specimens. Size given as 1.20 by .47 [inches; 30.5 by 11.9 mm], but the term "type" was not used.

Nomenclatural Remarks. Maynard (1920a: 80) first used the binomen *Strophiops santesoni* in error as one of three taxa that, in rare cases, can have a shell encircled by a band of color. Because this character is not diagnostic of *S. santesoni,* this passage cannot be considered a description of the taxon and the use is a nomen nudum. This use also includes a clearly incorrect reference to a subsequently published figure (Maynard, 1920b, fig. 59) that was captioned "*S. nuda* Mayn." Earlier on the same page is another reference to figure 59 that correctly refers to it as *S. nuda.* Maynard (1920d: 112) published a correction to the first use on page 80, stating "for *santesoni* read *persuasa.*" This statement makes it clear that the intended figure reference was figure 59* (Maynard, 1920b), which is captioned "*S. persuasa* M. & C. ×2, banded below suture." The next use of the name *S. santesoni* appeared in a discussion of sinistrality in Cerions (Maynard, 1920a: 81). Again, the text notes that this rare character is present in both *S. santesoni* and *S. inconstans,* and the use is a nomen nudum. However, it does include a reference to a subsequently published illustration (Maynard, 1920c, fig. 62) that was captioned "*S. santesoni.*" Because the publication of the association of a new species group name (Maynard, 1920a: 81) with an illustration (Maynard, 1920b, fig. 62) of the taxon being named before 1931 was interrupted, the name *Strophiops santesoni* became available only when the requirements of the relevant Articles (Articles 10.1.1 and 12.2.7, ICZN, 1999: 9, 17) have been met. The name *Strophiops santesoni* Maynard, 1920, became available July 10, 1920, on publication of figure 62, prior to the intended description of this species (Maynard and Clapp *in* Maynard, 1921b: 139, pl. 36, figs. 3, 4, pl. 15, fig. 5). Because of Maynard's unintended taxonomic act, both the date of publication and the authorship of *Strophiops santesoni* were altered.

Type Material. The unintended description linked the binomen *Strophiops santesoni* with a figure of a single sinistral specimen illustrated in Maynard, 1920c (fig. 62, pl. 15, fig. 5). Maynard (1920b: 81) noted that sinistrality is very rare in Cerion, and only two have been found, "one in *S. santesoni.*" This clearly indicates that he had multiple specimens of *C. santesoni,* of which one was sinistral, and suggests that the 1,964 specimens mentioned in the intended description of this taxon (Maynard and Clapp *in* Maynard, 1921a: 139) were available to him at the time and are thus part of the type series [Article 72.4.1.1, ICZN, 1999: 76]. *Strophiops santesoni* is thus based on 1,963 syntypes. Lot MCZ 76237 contained 216 specimens labeled "paratypes," among them the illustrated sinistral specimen, which is here designated as the lectotype and has been recatalogued as MCZ 358073. Maynard clearly regarded a different specimen to be the "Type" of *Strophiops santesoni.* Lot MCZ 76238 contains a single specimen labeled "Holotype" that resembles the illustration in the intended description, but differs substantially from the measure-

ments. This specimen is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures on plate 36. Maynard's remaining 1,962 specimens of *S. santesoni,* including MCZ 76237, MCZ 76238, USNM 420028, USNM 419959, and USNM 419964, are paralectotypes.

Lectotype Measurements. Length 23.5 mm, diameter (excluding lip) 11.2 mm; aperture height (including lip) 9.7 mm, aperture width (including lip and peristome) 7.9 mm.

Type Locality. Along northern shore of New Providence [Island] west of Nassau from second mile post to beyond the fourth.

Remarks. It is not surprising that, after Maynard's death, the specimens labeled as "types" by Maynard were the ones to be segregated at the MCZ, while the many remaining specimens were dispersed among MCZ, USNM, and other institutions (Turner, 1957: 151). Fortunately, the sinistral specimen originally illustrated by Maynard was segregated in a vial and labeled as the specimen appearing in figure 62. Surprisingly, the large lot collected by Maynard actually contained two sinistral specimens, both illustrated by Gould et al. (1985: 1368, fig. 1) as *Cerion glans* (Küster, 1844), New Providence sample. Gould and Woodruff (1986: 475) considered *S. santesoni* to be a synonym of *C. glans.*

Taxon 130. *Strophiops inconstans* Maynard, 1920b [April 8]: 81 [nomen nudum]; **Maynard, 1920c [July 10], fig. 63,** pl. 15, fig. 6; Maynard and Clapp *in* Maynard, 1920d: 119, pl. 3, figs. 7, 8. Examined 584 specimens. Size given as 1.10 by .40 [inches; 27.9 by 10.2 mm], but the term "type" was not used. Also 1920c [July 10], pl. 15, fig. 6.

Nomenclatural Remarks. The first use of the binomen *Strophiops inconstans* appeared in Maynard (1920b: 81) in a discussion of sinistrality in Cerionidae and referenced an illustration of a sinistral specimen published in the following issue (Maynard, 1920c, fig. 63). The identical image appeared in color in the later issue (Maynard, 1920c, pl. 15, fig. 6). Both illustrations were captioned "*S. inconstans.*" The use of *S. inconstans* in Maynard (1920b: 81) is a nomen nudum. For names published before 1931, the association of a new species group name with an illustration is sufficient to make the species group name available [Article 12.2.2.7, ICZN, 1999: 17]. Because of Maynard's unintended taxonomic act, the binomen *Strophiops inconstans* became available on July 10, 1920, with Maynard as the author. The intended description of this taxon was published in the subsequent issue (Maynard and Clapp *in* Maynard, 1920d: 119, pl. 3, figs. 7, 8) and was based on a dextral specimen.

Type Material. Although inadvertently, this taxon is based on a sinistral specimen illustrated in Maynard, 1920c (fig. 63, pl. 15, fig. 6). It is likely that the 584 specimens mentioned in the intended description of this taxon (Maynard and Clapp *in* Maynard, 1921a: 131) were available to Maynard at the time and are thus part of the type series [Article 72.4.1.1, ICZN, 1999: 76]. *Strophiops inconstans* is based on 584 syntypes. Lot MCZ 76341 contained multiple specimens labeled "paratypes," among them the illustrated sinistral specimen, which is here designated as the lectotype of *Strophiops inconstans* and has been recatalogued as MCZ 356677. Maynard clearly regarded a different specimen to be the "Type" of *Strophiops inconstans.* Lot MCZ 76340 contained a single specimen labeled "Holotype" that approximates the measurements and illustrations of this taxon in the intended description. This specimen is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures in the intended description. It becomes a paralectotype, as do the specimens in MCZ 76340, MCZ 76341, and USNM 420121.

Lectotype Measurements. Length 26.4

mm, diameter (excluding lip) 11.2 mm; aperture height (including lip) 7.6 mm, aperture width (including lip and peristome) 7.9 mm.

Type Locality. West side of Bird Key [Exuma Group, Bahamas].

Remarks. It is not surprising that, after Maynard's death, the specimens labeled as "types" by Maynard were the ones to be segregated at the MCZ, while the many remaining specimens were dispersed among MCZ, USNM, and other institutions (Turner, 1957: 151). Fortunately, the sinistral specimen was retained among the material at the MCZ and was easily recognized. Maynard (1920d: 119) reported *Strophiops inconstans* to be common on cacti. Maynard (1925: 185–194) provided additional information on the anatomy, habitat, and morphology of this taxon.

Taxon 131. *Strophiops plebeia* Maynard, 1920b [April 8]: 85 [nomen nudum]. *Strophiops plebea* **Maynard 1920c [July 10], fig. 66, pl. 14, fig. 1.** *Strophiops plebia* Maynard and Clapp *in* Maynard, 1921a [May 2]: 130, pl. 28, figs. 3, 4. Examined 1,500 specimens. Size given as 1.20 by .40 [inches; 30.5 by 11.4 mm], but the term "type" was not used.

Nomenclatural Remarks. This binomen was first used by Maynard (1920b: 85) [as *plebeia*] as an example of a fairly commonly decollated species [80 of 1,500 specimens] and included a reference to an illustration of an apertural view of a shell published in the following issue (Maynard 1920c, fig. 66, pl. 14, fig. 1). Both the text illustration and the identical colored figure were captioned "*S. plebea.*" The April 8, 1920, use as *plebeia* is a nomen nudum. The association of a new species group name with an illustration of the taxon being named before 1931 makes the name *Strophiops plebea* Maynard (1920c, fig. 66, pl. 14, fig. 1) available (Article 12.2.7, ICZN, 1999: 17) prior to the intended description of this species (Maynard and Clapp *in* Maynard, 1921a: 131, pl. 28, figs. 7, 8).

Type Material. Although the unintended description of *Strophiops plebea* makes reference only to a single decollated specimen illustrated in figure 66, it is likely that the 1,500 specimens mentioned in the intended description of this taxon (Maynard and Clapp *in* Maynard, 1921a: 130) were available to Maynard at the time and are thus part of the type series [Article 72.4.1.1, ICZN, 1999: 76]. *Strophiops plebea* is based on 1,500 syntypes.

In a search for the specimen illustrated in figure 66, examination of large series of this taxon from the Maynard collection now at the MCZ and USNM revealed over 25 decollated specimens. About a third of these specimens could be excluded from consideration on the basis of the degree of decollation or the presence of other damage undocumented in the illustration. The majority of decollated specimens, however, all resembled the illustration to a similar degree, and we are not able to match any one of them to the illustration with any degree of certainty.

Maynard clearly regarded a different specimen to serve as the "Type" of *Strophiops plebea.* Lot MCZ 76401 was labeled "Holotype," but contained two specimens, neither a close match to the figures or measurements in the intended taxon description. Nor were any labels in Maynard's handwriting present. Lot USNM 420125 contained numerous specimens from among the 1,500 syntypes. A specimen that closely approximates the illustrations and measurements published together with the intended taxon description was selected as a lectotype (USNM 420125) to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining specimens were recatalogued as USNM 1093795, and together with MCZ 76401 and MCZ 76169, are paralectotypes.

Lectotype Measurements. Length 30.9 mm, diameter (excluding lip) 11.3 mm; ap-

erture height (including lip) 10.3 mm, aperture width (including lip and peristome) 8.7 mm.

Type Locality. Lignumvitae Key, Berry Islands, Bahamas.

Remarks. This taxon has been the victim of multiple lapsus calami, having been spelled *plebeia* when first used as a nomen nudum, *plebea* in the unintended, but valid description, and *plebia* in the intended taxonomic description, as well as in a subsequent listing in the sales catalogue (Maynard, 1924?: 3). Article 32.5.1 (ICZN, 1999: 39) dictates that the spelling *plebea* be used for this taxon because there is no clear evidence to suggest an alternative spelling within the original publication itself. *Strophiops plebea* Maynard, 1920, has a different spelling, authorship, and date of publication from that cited by Clench (1957: 158).

Taxon 132. *Strophiops cana* Maynard, 1920b [April 8]: 86, 88 [nomen nudum]; **Maynard and Clapp *in* Maynard, 1920c [July 10], figs. 69, 76, pl. 15, fig. 1, pl. 17, fig. 5**; Maynard and Clapp *in* Maynard, 1921a [May 2]: 137; 1921b [July 15], pl. 34, figs. 3, 4. Examined 760 specimens. Size given as 1.10 by .45 [inches; 27.9 by 11.4 mm], but the term "type" was not used.

Nomenclatural Remarks. The binomen *Strophiops cana* was first used by Maynard (1920b: 86, 88) in a discussion of shell repair after severe damage and referred to subsequently published illustrations (Maynard, 1920c, figs. 69, 76, pl. 15, fig. 1, pl. 17, fig. 5) of damaged specimens of *S. cana* as examples of snails surviving crushing predation, noting that color change occasionally accompanied shell repair. The appearances of *S. cana* in the text (Maynard, 1920b: 86, 88) are as a nomen nudum. The association of a new species group name with an illustration of the taxon being named before 1931 made the name *Strophiops cana* Maynard and Clapp *in* Maynard, 1920, available (Article 12.2.7, ICZN, 1999: 17) on July 10, with the publication of figures 69 and 76, the first captioned "*S. cana* M & C" and the second "*S. cana,*" prior to the intended description of this species (Maynard and Clapp *in* Maynard, 1921a: 137).

Type Material. In addition to the two damaged specimens of *Strophiops cana* that were illustrated in figures 69 and 76 (as well as the colored versions of these figures, pl. 15, fig. 1, pl. 17, fig. 5), it is likely that the 760 specimens mentioned in the intended description of this taxon (Maynard and Clapp *in* Maynard, 1921a: 137) were available to Maynard at the time and are thus part of the type series [Article 72.4.1.1, ICZN, 1999: 76]. *Strophiops cana* is based on 760 syntypes. Neither of the specimens illustrated in figures 69 and 76 could be located at the MCZ. Maynard clearly regarded a different specimen to be the "Type" of *Strophiops cana.* Lot MCZ 76374 contains a single specimen labeled "Holotype" that approximates the measurements of this taxon in the intended description (Maynard and Clapp *in* Maynard, 1921a: 137) and the subsequently published illustrations (Maynard, 1921b, pl. 34, figs. 3, 4) and is accompanied by a label in Maynard's hand with the term "type" that includes references to the figures. This specimen (MCZ 76374) is here designated as the lectotype of *Strophiops cana* Maynard and Clapp *in* Maynard, 1920, to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining specimens, including MCZ 76373, MCZ 118217, and USNM 420091, are paralectotypes.

Lectotype Measurements. Length 28.3 mm, diameter (excluding lip) 11.5 mm; aperture height (including lip) 10.1 mm, aperture width (including lip and peristome) 8.9 mm.

Type Locality. Fortune Key, Berry Islands, Bahamas.

Remarks. It is not surprising that, after Maynard's death, the specimens labeled as "types" by Maynard were the ones to be

segregated at the MCZ, while the many remaining specimens, possibly including those in figures 69 and 76, were dispersed among MCZ, USNM, and other institutions (Turner, 1957: 151).

Taxon 133. *Strophiops territa* **Maynard, 1920c [July 10], fig. 70*, pl. 15, fig. 2**; Maynard, 1920d: 112; Maynard and Clapp *in* Maynard, 1921b: 147; Maynard, 1926, pl. 43, figs. 5, 6. Examined 393 specimens. Size given as .94 by .40 [inches; 23.9 by 10.2 mm], but the term "type" was not used.

Nomenclatural Remarks. The binomen *Strophiops territa* was first used by Maynard (1920c, fig. 70*, pl. 15, fig. 2) in the caption to a figure of an apertural view of a crushed and repaired shell. Figure 70* and the identical colored image on plate 15, figure 2, are both captioned "*S. territa* M."; the authorship of the taxon is restricted to Maynard. The association of a new species group name with an illustration of the taxon being named before 1931 makes the name *Strophiops territa* Maynard, 1920c (fig. 70*, pl. 15, fig. 2), available (Article 12.2.7, ICZN, 1999: 17) on July 10, 1920, prior to the intended description of this species (Maynard and Clapp *in* Maynard, 1921b: 147).

Type Material. Although the unintended description of *Strophiops territa* makes reference only to a single damaged specimen shown in figure 70*, it is likely that the 393 specimens mentioned in the intended description of this taxon (Maynard and Clapp *in* Maynard, 1921b: 147) were available to Maynard at the time and are thus part of the type series [Article 72.4.1.1, ICZN, 1999: 76]. *Strophiops territa* is based on 393 syntypes. The specimen illustrated in figure 70* could not be located at the MCZ. Maynard clearly regarded a different specimen to be the "Type" of *Strophiops territa.* Lot MCZ 76396 contains a single specimen labeled "Holotype" that approximates the measurements of this taxon in the intended description and the subsequently published illustrations. It is accompanied by a label in Maynard's hand with the term "type," that includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 392 specimens, including MCZ 76316 and USNM 419995, are paralectotypes.

Lectotype Measurements. Length 23.4 mm, diameter (excluding lip) 11.3 mm; aperture height (including lip) 9.3 mm, aperture width (including lip and peristome) 8.1 mm.

Type Locality. Methodist Churchyard and vicinity [Sherley Street, Nassau, New Providence Island, Bahamas].

Remarks. It is not surprising that, after Maynard's death, the specimens labeled as "types" by Maynard were the ones to be segregated at the MCZ, while the many remaining specimens, possibly including the damaged specimen in figure 70*, were dispersed among MCZ, USNM, and other institutions (Turner, 1957: 151). Gould and Woodruff (1986: 476) regarded this taxon to be an "anomalously located species attributable to *Cerion glans.*"

Taxon 134. *Strophiops albolabra* Maynard, 1919b [November 6]: 25 [nomen nudum]; Maynard, 1920b [April 8]: 87, 88 [nomina nuda]; **Maynard, 1920c [July 10], figs. 74a, b, 75, 77, pl. 16, figs. 1–3, pl. 17, fig. 4**; Maynard and Clapp *in* Maynard, 1921a [May 2]: 129–130, pl. 27, figs. 3, 4. Examined 4,560 specimens. Size given as 1.30 by .50 [inches; 33.0 by 12.7 mm], but the term "type" was not used.

Nomenclatural Remarks. The binomen *Strophiops albolabra* first appeared as a nomen nudum (Maynard, 1919b: 25). Maynard (1920b: 87, 88) discussed shell repair in this species prior to its intended description and included citations to illustrations of four broken specimens that

were published in the following issue (Maynard, 1920c [July 10], figs. 74a, b, 75, 77). These same figures were reproduced in color in the same issue (Maynard, 1920c, pl. 16, figs. 1–3, pl. 17, fig. 4). The appearances of the taxon name in the text are as a nomen nudum.

The association of a new species group name with an illustration of the taxon being named before 1931 makes the name *Strophiops albolabra* Maynard, 1920c (figs. 74a, b, 75, 77, pl. 16, figs. 1–3, pl. 17, fig. 4), available (Article 12.2.7, ICZN, 1999: 17) on July 10, 1920, prior to the intended description of this species (Maynard and Clapp *in* Maynard, 1921a: 129–130). Because the illustrations were captioned "*S. albolabra,*" the taxon must be attributed to Maynard rather than Maynard and Clapp as cited by Clench (1957: 137).

Type Material. Although the unintended description of *Strophiops albolabra* illustrated four broken specimens, it is likely that these were selected from among the 4,560 specimens mentioned in the intended description of this taxon (Maynard and Clapp *in* Maynard, 1921a: 130) that were available to Maynard and are part of the type series [Article 72.4.1.1, ICZN, 1999: 76]. *Strophiops albolabra* is based on 4,560 syntypes. Over a thousand specimens contained in MCZ 76241, MCZ 118211, USNM 420023, and USNM 420098 were examined. Only two exhibited significant shell damage but did not correspond to any of the four figured syntypes. These four syntypes are lost because it is unlikely that badly damaged specimens would have been selected for sale or exchange by Maynard. Maynard clearly regarded a different specimen to be the "Type" of *Strophiops albolabra.* Lot MCZ 76255 contains a single specimen labeled "Holotype" that approximates the illustration more than the measurements of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures in the intended taxon description (Maynard, 1921a, pl. 27, figs. 3, 4). This specimen is here designated as the lectotype of *Strophiops albolabra* to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 4,559 specimens are paralectotypes.

Lectotype Measurements. Length 29.7 mm, diameter (excluding lip) 12.4 mm; aperture height (including lip) 11.0 mm, aperture width (including lip and peristome) 9.1 mm.

Type Locality. Great Harbor Key [Berry Islands, Bahamas].

Remarks. It is not surprising that, after Maynard's death, the specimens labeled as "types" by Maynard were the ones to be segregated at the MCZ, while the many remaining specimens were dispersed among MCZ, USNM, and other institutions (Turner, 1957: 151). The four severely damaged syntypes would be easily recognizable, yet could not be found in the collections of the MCZ and might have been discarded, especially since in excess of 4,000 specimens were available.

Taxon 135. *Strophiops fragilis* Maynard, 1920b [April 8]: 91, 92 [nomen nudum]; **Maynard, 1920c [July 10], figs. 81, 82, pl. 18, figs. 4, 5**; Maynard and Clapp *in* Maynard, 1921a [May 2]: 128, pl. 26, figs. 3, 4. Examined 200 specimens. Size given as 1.00 by .40 [inches; 25.4 by 10.2 mm], but the term "type" was not used.

Nomenclatural Remarks. Maynard (1920b: 91–92) used the binomen *Strophiops fragilis* prior to its intended description as an example of his "Law of Individual Reincarnation" and referenced subsequently published illustrations (Maynard, 1920c, figs. 81, 82) representing apertural views of two different specimens that were reproduced in color (Maynard, 1920c, pl. 18, figs. 4, 5). Article 10.1.1 (ICZN, 1999: 9) states that if publication of the data relating to a new nominal taxon or a nomenclatural act is interrupted and

continued at a later date, the name or act becomes available only when the requirements of the relevant Articles have been met. Thus, the first uses of the name (Maynard, 1920b: 91–92) were nomina nuda. The association of a new species group name with an illustration of the taxon being named before 1931 makes the name *Strophiops fragilis* Maynard, 1920c (figs. 81, 82, pl. 18, figs. 4, 5), available (Article 12.2.7, ICZN, 1999: 17) on July 10, 1920, prior to the intended description of this species (Maynard and Clapp *in* Maynard, 1921a: 128). As the illustrations were captioned "*S. fragilis,*" the taxon must be attributed to Maynard rather than Maynard and Clapp as cited by Clench (1957: 146).

Type Material. Two different specimens of *S. fragilis* were illustrated (Maynard, 1920c, figs. 81, 82, pl. 18, figs. 4, 5). One (fig. 81, pl. 18, fig. 4) was reported to closely resemble *S. agrestina* (figs. 80, pl. 18, fig. 3) the other (fig. 82, pl. 18, fig. 5) was described as indistinguishable from *S. nuda* (fig. 83, pl. 18, fig. 6). These two specimens were selected from the 200 specimens mentioned in the intended description of this taxon (Maynard and Clapp *in* Maynard, 1921a: 128) that were available to Maynard and are part of the type series [Article 72.4.1.1, ICZN, 1999: 76]. *Strophiops territa* is based on 200 syntypes. Lot MCZ 76166 contains a single specimen labeled "Holotype" that is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures in the intended description (pl. 26, figs. 3, 4). Although this specimen closely matches the measurements provided in the subsequent description, it more closely resembles one of the two illustrations (Maynard, 1920c, fig. 81, pl. 18, fig. 4) on which the taxon is based than it does the subsequent illustration in the intended description. In our view, it is probable that this specimen served as the basis for both illustrations. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining syntypes become paralectotypes.

Lectotype Measurements. Length 25.5 mm, diameter (excluding lip) 10.2 mm; aperture height (including lip) 9.4 mm, aperture width (including lip and peristome) 8.1 mm.

Type Locality. Second westernmost Brigadier Key, Great Exuma [Exuma Group, Bahamas].

Remarks. Maynard (1920c: 92) commented that five specimens of *S. fragilis* were indistinguishable from *S. nuda* [from Clarence Harbor, Long Island, Bahamas].

Taxon 136. *Strophiops latonia* **Maynard, 1920c [July 10]: 95, fig. 84, pl. 18, fig. 1**; Maynard and Clapp *in* Maynard, 1921b [July 15]: 147–148; Maynard and Clapp *in* Maynard, 1926 [March 24], pl. 43, figs. 7, 8. Examined 600 specimens. Size given as 1.10 by .42 [inches; 27.9 by 10.7 mm], but the term "type" was not used.

Nomenclatural Remarks. The binomen *Strophiops latonia* was used prior to its intended description (Maynard, 1920c: 95, fig. 84) as an example of the "Law of Specific Reincarnation." The figure was reproduced in color (Maynard, 1920c, pl. 18, fig. 1). The association of a new species group name with an illustration of the taxon being named before 1931 makes the name *Strophiops latonia* available (Article 12.2.7, ICZN, 1999: 17) at the time of publication of the illustrations (July 10, 1920) rather than on July 15, 1921, when the intended original description was published. As these illustrations were captioned "*S. latonia,*" the taxon is attributed to Maynard, rather than Maynard and Clapp, as cited by Clench (1957: 150).

Type Material. Although the unintended description of *Strophiops latonia* is based on the illustration of a single specimen (fig. 84), it is likely that the 600 specimens mentioned in the intended description of

this taxon (Maynard and Clapp *in* Maynard, 1921b: 148) were available to Maynard at the time and are thus part of the type series [Article 72.4.1.1, ICZN, 1999: 76]. *Strophiops latonia* is therefore based on 600 syntypes. The specimen shown in figure 84 could not be located at the MCZ. Maynard clearly regarded a different specimen to be the "Type" of *Strophiops latonia.* Lot MCZ 76314 contains a single specimen labeled "Holotype" that approximates the measurements of this taxon in the intended description (Maynard, 1921b: 147–148) and the subsequently published illustrations (Maynard, 1926, pl. 43, figs. 7, 8) and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen (MCZ 76314) is here designated as the lectotype of *Strophiops latonia* Maynard, 1920, to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining specimens, including MCZ 76315 and USNM 420146, are paralectotypes.

Lectotype Measurements. Length 28.1 mm, diameter (excluding lip) 10.8 mm; aperture height (including lip) 9.6 mm, aperture width (including lip and peristome) 8.0 mm.

Type Locality. St. Paul's Quarry off West Sherley Street, Nassau [New Providence Island, Bahamas].

Remarks. Maynard (1924c: 6) listed *S. latonia* as extinct in 1924 from the burning of vegetation prior to cultivation. Gould and Woodruff (1986: 476) regarded this taxon to be "intermediate" between *Cerion glans* (Küster, 1844) and *C. gubernatorium* (Crosse, 1869).

Taxon 137. *Strophiops mariae* **Maynard and Clapp *in* Maynard, 1920c [July 10]: 96, fig. 88**; Maynard, 1920d [September 30], pl. 24, fig. 10 [apertural view of costate specimen], pl. 25, fig. 5 [left lateral view of smooth specimen]; Maynard and Clapp *in* Maynard, 1921a [May 2]: 128. Examined 216 specimens [96 smooth and 120 costate]. Size given as 1.10 by .40 [inches; 27.9 by 10.2 mm], but the term "type" was not used.

Nomenclatural Remarks. The taxon name *Strophiops mariae* was first used and figured by Maynard (1920c: 96, fig. 88) as an example of his "Law of Specific Reincarnation" earlier than the intended description of the species. The association of a new species group name with an illustration of the taxon being named before 1931 makes the name *Strophiops mariae* available (Article 12.2.7, ICZN, 1999: 17) prior to the intended description of this species (Maynard and Clapp *in* Maynard, 1921a: 128). The illustrations referenced in the intended description were published in the previous issue (Maynard, 1920d, pl. 24, fig. 10, pl. 25, fig. 5) and depict two different specimens. Because figure 88 is captioned "*S. mariae* M & C.," the taxon is attributed to Maynard and Clapp *in* Maynard and dates from July 10, 1920.

Type Material. Although the unintended description of *Strophiops mariae* is based on the illustration of a single specimen (fig. 88), it is likely that the 216 specimens mentioned in the intended description of this taxon (Maynard and Clapp *in* Maynard, 1921a: 128) were available to Maynard at the time and are thus part of the type series [Article 72.4.1.1, ICZN, 1999: 76]. *Strophiops mariae* is therefore based on 216 syntypes. The specimen shown in figure 84 could not be located at the MCZ. Lot MCZ 76204 contains 120 specimens and was labeled "Paratypes." Of these 120 specimens, two were sequestered in glass vials and labeled as figured specimens. One of the labels in Maynard's handwriting associated with the smooth specimen illustrated on plate 25, figure 5, states "Fig. 88." This specimen, which retains the number MCZ 76204, is here designated as the lectotype of *Strophiops mariae* Maynard and Clapp *in* Maynard, 1920, to provide an objective standard of reference for this species-group taxon that is consistent

with Maynard's original concept of it. The remaining 119 specimens were recatalogued as MCZ 357002 and, together with MCZ 118193, are among the 215 specimens that become paralectotypes.

Lectotype Measurements. Length 27.8 mm, diameter (excluding lip) 10.1 mm; aperture height (including lip) 9.7 mm, aperture width (including lip and peristome) 8.0 mm.

Type Locality. Maria Key near Little Exuma [Exuma Group, Bahamas].

Remarks. Maynard (1920c: 96) noted that the species *S. mariae* closely resembles *S. repetita* from Nassau, New Providence Island.

Taxon 138. *Strophiops repitita* Maynard, 1919b: 36 [nomen nudum]; *S. repetita* **Maynard and Clapp *in* Maynard, 1920c [July 10]: 96, fig. 89**; Maynard and Capp *in* Maynard, 1921b [July 15]: 149, pl. 45, figs. 5, 6 [pl. 45 was never issued]. Examined 1,052 specimens. Size given as 1.10 by .40 [inches; 27.9 by 10.2 mm], but the term "type" was not used.

Nomenclatural Remarks. The binomen *S. repitita* first appeared as a nomen nudum (Maynard, 1919b: 36). The name was used as *S. repetita* (Maynard, 1920c: 96, fig. 89) prior to the intended taxon description as an example of Maynard's "Law of Specific Reincarnation." The association of a new species group name with an illustration of the taxon being named before 1931 makes the name *Strophiops repetita* Maynard and Clapp *in* Maynard, 1920, available (Article 12.2.7, ICZN, 1999: 17) prior to the intended description of this species (Maynard and Clapp *in* Maynard, 1921b: 149). The caption to figure 89 reads "*S. repetita* M & C.," establishing the authorship as Maynard and Clapp *in* Maynard, 1920.

Type Material. The unintended description of *Strophiops repetita* is based on the illustration of a single specimen (fig. 89). It is likely that this was one of 1,052 specimens mentioned in the intended description of this taxon (Maynard and Clapp *in* Maynard, 1921b: 149) that were available to Maynard at the time and are thus part of the type series [Article 72.4.1.1, ICZN, 1999: 76]. *Strophiops repetita* is therefore based on 1,052 syntypes. No specimen labeled as the "Holotype" of *Strophiops repetita* was catalogued at the MCZ. Lot MCZ 76336 contained 198 specimens and was labeled "Paratypes." A single specimen was sequestered in a vial and labeled "figured." This specimen closely approximates both the illustration in figure 89 and the measurements in the intended description. Also present was a label in Maynard's handwriting referring to "Fig 89" and "Plate 45 figs 5–6." This label indicates that the sequestered specimen is that in figure 89, as well as the specimen that Maynard regarded as the "type" because he planned to illustrate it as part of the intended taxon description. This specimen, which retains the number MCZ 76336 is here designated as the lectotype of *Strophiops repetita* Maynard and Clapp *in* Maynard, 1920, to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 197 specimens were recatalogued as MCZ 357003 and are among the remaining 1,051 specimens that become paralectotypes.

Lectotype Measurements. Length 27.3 mm, diameter (excluding lip) 10.4 mm; aperture height (including lip) 9.3 mm, aperture width (including lip and peristome) 8.0 mm.

Type Locality. Old fields off Kemp's Road, East Nassau [New Providence Island, Bahamas].

Remarks. The spelling *Strophiops repitita* appeared only as a nomen nudum (Maynard, 1919b: 36). Both the unintended and the intended taxon descriptions used the spelling *S. repetita.* The sales catalog (Maynard, 1924b?: [4]) used the spell-

ing *repitita*, but its supplement (Maynard, 1924c: 6) listed *S. repetita* as nearly extinct (only three specimens) in 1924 from the burning of vegetation prior to cultivation. Gould and Woodruff (1986: 477) regarded this taxon to be a synonym of *Cerion gubernatorium* (Crosse, 1869).

Taxon 139. *Strophiops perantiqua* Maynard, 1919a [October 16]: 15 [nomen nudum]; Maynard, 1919b [November 6]: 31 [nomen nudum]; **Maynard and Clapp *in* Maynard, 1920d [September 30]: 115, pl. 1, figs. 1, 2, map 1, 2** [published as map 1, 1]. Examined 25 specimens. Size given as 1.25 by .60 [inches; 31.8 by 15.2 mm], but the term "type" was not used.

Nomenclatural Remarks. Maynard's (1919a: 15) first use of this binomen was a nomen nudum. Maynard (1919b: 31) again used this name, this time along with a reference to illustrations that were issued later (Maynard, 1920d, pl. 1, figs. 1, 2), together with the intended taxon description. The second use of the name in 1919 was again a nomen nudum. Article 10.1.1 (ICZN, 1999: 9) states that if publication of the data relating to a new nominal taxon or a nomenclatural act is interrupted and continued at a later date, the name or act becomes available only when the requirements of the relevant Articles have been met. Thus, the name *S. perantiqua* becomes available on September 30, 1920, upon publication of the illustrations but does not have priority over the simultaneously published intended taxon description, which references the same illustrations. The taxon *S. perantiqua* dates from the intended species description (Maynard and Clapp *in* Maynard, 1920d: 115, pl. 1, figs. 1, 2), as cited by Clench and Aguayo (1952). *Strophiops perantiqua* is an junior objective synonym of *Strophiops peravita* Maynard, 1919, because they share the same type series, including the same lectotype [see Taxon 114].

Type Material. The taxon description by Maynard and Clapp *in* Maynard, 1920d (p. 115) did not distinguish among the 25 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in the original description or in any of Maynard's publications to associate a single specimen with the term "type." Clench and Aguayo (1952: 440, pl. 55, fig. 6) listed and illustrated MCZ 187537 as the "holotype," but the specimen is not accompanied by Maynard's label. Article 74.5 (ICZN, 1999: 82) states, "When the original work reveals that the taxon had been based on more than one specimen, a subsequent use of the term 'holotype' does not constitute a valid lectotype designation unless the author, when wrongly using that term, explicitly indicated that he or she was selecting from the type series that particular specimen to serve as the name-bearing type." Thus, there is no holotype for this taxon, nor can Clench and Aguayo's treatment of MCZ 187537 be considered a lectotype designation. The species is based on 25 syn-

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Figures 138–150. Taxon 138. *Strophiops repetita* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76336. Old fields off Kemp's Road, East Nassau, New Providence Island, Bahamas. Taxon 139. *Strophiops perantiqua* Maynard and Clapp *in* Maynard, 1920. [Not illustrated.] The binomen *Strophiops perantiqua* is an objective junior synonym of *Strophiops peravita* Maynard, 1919 [Taxon 114], as the lectotype of *Strophiops peravita* is also the lectotype of *S. perantiqua.* Taxon 140. *Strophiops processa* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76148. In area just south of the third beach north of the south end of Great Guana Key Exumas, Bahamas. Taxon 141. *Strophiops mutatoria* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76234. Northwest of small pond near south end of Great Guana Key, Exuma Group, Bahamas. Taxon 142. *Strophiops mitra* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 187538. Back of fourth beach from south end of Great Guana Key, Exuma Group, Bahamas. Taxon 143. *Strophiops intentata* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76305. Small area east or tract 5 just south of the third beach north of the south end of Great Guana Key, Exumas, Bahamas. Taxon 144. *Strophiops prognata* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76163. Between small pond and beach, southern end of Great Guana Key, Exuma Group, Bahamas. Taxon 145. *Strophiops extrema* Maynard and Clapp *in* Maynard, 1920.

Lectotype MCZ 76146. Near well, at extreme south end of Great Guana Key, Exuma Group, Bahamas. Taxon 146. *Strophiops imperfecta* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76313. Near well on south end of Great Guana Key, Exuma Group, Bahamas. Taxon 147. *Strophiops progressa* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76197. Near Black Point, north end of Great Guana Key, Exuma Group, Bahamas. Taxon 148. *Strophiops cyclura* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76045. Bitter Guana Key, Exuma Group, Bahamas. Taxon 149. *Strophiops dissimila* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76057. East Cistern Key, Exuma Group, Bahamas. Taxon 150. *Strophiops veta* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76221. Strout's [Stroud's] Key, Exuma Group, Bahamas.

types. Of these, MCZ 187537 (the lectotype of *Strophiops peravita* [Taxon 114]), which closely approximates the published measurements and clearly matches the published illustrations, is here designated as the lectotype of *Strophiops perantiqua* to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original and Clench and Aguayo's subsequent concepts of this taxon. The remaining 24 syntypes become paralectotypes.

Lectotype Measurements. Length 31.9 mm, diameter (excluding lip) 14.7 mm; aperture height (including lip) 11.1 mm, aperture width (including lip and peristome) 9.5 mm.

Type Locality. Found fossil in red earth near west coast of Great Guana Key [Exumas, Bahamas], about 1 mile from southern end.

Remarks. Maynard (1924a: 164) described in detail the locality in which these fossils were collected. Clench and Aguayo (1952) considered *Cerion perantiquum* to be a hybrid between the "*scalarinum* element and a member of the *glans* complex."

Taxon 140. *Strophiops processa* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 116, pl. 1, figs. 7, 8, map 1, 5.** Examined 300 specimens. Size given as .85 by .35 [inches; 26.9 by 7.6 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 300 specimens examined. Later, Maynard (1924a: 168) wrote that only 122 were collected. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in the original description or in any of Maynard's publications to associate a single specimen with the term "type." Clench and Aguayo (1952: 431, pl. 56, fig. 3) listed and illustrated MCZ 76148 as the "holotype," presumably on the basis of a handwritten label accompanying the specimen with the term "typical." Article 74.5 (ICZN, 1999: 82) states, "When the original work reveals that the taxon had been based on more than one specimen, a subsequent use of the term 'holotype' does not constitute a valid lectotype designation unless the author, when wrongly using that term, explicitly indicated that he or she was selecting from the type series that particular specimen to serve as the name-bearing type." Thus, there is no holotype for this taxon, nor can Clench and Aguayo's treatment of MCZ 76148 be considered a lectotype designation. The species is based on either 300 or 122 syntypes. Of these, MCZ 76148 is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original and Clench and Aguayo's subsequent concepts of this taxon. The remaining 121 or 299 syntypes become paralectotypes.

Lectotype Measurements. Length 24.4 mm, diameter (excluding lip) 8.8 mm; aperture height (including lip) 8.5 mm, aperture width (including lip and peristome) 7.5 mm.

Type Locality. In area just S of the third beach north of the south end of Great Guana Key [Exumas, Bahamas].

Remarks. Maynard (1920d: 116) reported that this taxon was rather common, but all 300 specimens collected were dead. Maynard (1924a: 168) later contradicted this number, stating that 122 specimens were collected. Clench and Aguayo (1952: 431) considered this taxon to be a subspecies of *Cerion asperum* (Maynard, 1920).

Taxon 141. *Strophiops mutatoria* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 116, pl. 1, figs. 3, 4, map 1, 6**; Maynard, 1924a: 170. Examined 500 specimens. Size given as 1.00 by .26 [inches; 25.4 by 6.6 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 500 speci-

mens examined. Later, Maynard (1924a: 170) wrote that 627 were collected. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in the original description or in any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 500 or 627 syntypes. Of these, MCZ 76234 was labeled "Holotype-command." and contains a single specimen accompanied by a note in Maynard's handwriting with the term "type." This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 499 or 626 syntypes become paralectotypes.

Lectotype Measurements. Length 25.9 mm, diameter (excluding lip) 7.4 mm; aperture height (including lip) 7.6 mm, aperture width (including lip and peristome) 6.4 mm.

Type Locality. In area south of last [*Strophiops processa* = area just south of the third beach north of the south end of Great Guana Key, Exuma Group, Bahamas].

Remarks. Maynard (1920d: 116) reported this taxon to be common, but all 500 specimens examined were collected dead. Later, Maynard (1924a: 170) reported that 623 specimens were collected dead, of which two were fossilized.

Taxon 142. *Strophiops mitra* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 118, pl. 2, figs. 4, 5, map 1, 1.** Examined 75 specimens. Size given as 1.25 by .50 [inches; 31.8 by 12.7 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 75 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in the original description or in any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 75 syntypes. Of these, MCZ 187538, which was labeled "Holotype" and contains a single specimen, is here designated as the lectotype to provide an objective standard of reference for this species-group taxon. The remaining 74 syntypes become paralectotypes.

Lectotype Measurements. Length 31.2 mm, diameter (excluding lip) 13.7 mm; aperture height (including lip) 12.2 mm, aperture width (including lip and peristome) 9.9 mm.

Type Locality. Back of fourth beach from south end of Great Guana Key [Exuma Group, Bahamas], under fallen palm fronds.

Remarks. Maynard (1924a: 170) provided supplemental information on the shell, animal, anatomy, and habitat.

Taxon 143. *Strophiops intentata* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 118, pl. 2, figs. 6, 7, map 1, 7**; Maynard, 1925: 171. Examined 256 specimens. Size given as .75 by .30 [inches; 19.1 by 7.6 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 256 specimens examined. Later, Maynard (1925: 171) wrote that 239 were collected. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in the original description or in any of Maynard's publications to associate a single specimen with the term "type." Clench and Aguayo, (1952: 431, pl. 56, fig. 4) identified and illustrated MCZ 76305 as "holotype," presumably on the basis of a handwritten label identifying a type specimen. Article 4.5 (ICZN, 1999: 82) states, "When the orig-

inal work reveals that the taxon had been based on more than one specimen, a subsequent use of the term 'holotype' does not constitute a valid lectotype designation unless the author, when wrongly using that term, explicitly indicated that he or she was selecting from the type series that particular specimen to serve as the name-bearing type." Thus, there is no holotype for this taxon, nor can Clench and Aguayo's treatment of MCZ 76305 be considered a lectotype designation. The species is based on 256 or 239 syntypes. Of these, MCZ 76305 is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original and Clench and Aguayo's subsequent concepts of it. The remaining 255 or 238 syntypes become paralectotypes.

Lectotype Measurements. Length 20.3 mm, diameter (excluding lip) 8.4 mm; aperture height (including lip) 7.3 mm, aperture width (including lip and peristome) 6.8 mm.

Type Locality. Rather common in a small area east of tract 5 [= type locality of *Strophiops processa* = area just south of the third beach north of the south end of Great Guana Key, Exumas, Bahamas].

Remarks. Maynard (1920d: 118) reported that all of the 256 specimens were collected dead and some were very old. Maynard (1925: 170) reported that 239 specimens were collected. Clench and Aguayo (1952: 431) listed this taxon in the synonymy of *Cerion asperum processum* (Maynard and Clapp, 1920) [Taxon 140].

Taxon 144. *Strophiops prognata* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 118, pl. 2, figs. 8, 9, map 1, 8**; Maynard, 1924: 171–172. Examined 300 specimens. Size given as .92 by .40 [inches; 23.4 by 10.2 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 300 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in the original description or in any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 300 syntypes. Of these, MCZ 76163, which was labeled "Holotype" and contains a single specimen accompanied by a note in Maynard's handwriting with the term "type," is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 299 syntypes become paralectotypes.

Lectotype Measurements. Length 22.9 mm, diameter (excluding lip) 9.8 mm; aperture height (including lip) 9.0 mm, aperture width (including lip and peristome) 7.6 mm.

Type Locality. Common in area between a small pond P [map 1, 8, p. 117] and beach. [Southern end of Great Guana Key, Exuma Group, Bahamas.]

Remarks. Maynard (1920d: 118) reported that all 300 specimens were collected dead, but were more recent than *Strophiops intentata.* Maynard (1924: 171–172) added some additional information, but did not mention the number collected.

Taxon 145. *Strophiops extrema* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 118,** pl. 3, figs. 1, 2 [these figures are cited in the original description but captioned "*S. imperfecta*"], **pl. 2, figs. 10, 11** [these figures are not cited in the original description but are captioned "*S. extrema* M. & C."], **map 1, 9**; Maynard, 1924: 173. Examined 150 specimens. Size given as 1.05 by .49 [inches; 26.7 by 12.4 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 150 specimens examined. In the preamble to the

taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in the original description or in any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 150 syntypes. Of these, MCZ 76146, which was labeled "Holotype" and contains a single specimen accompanied by a note in Maynard's handwriting with the term "type," is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 149 syntypes become paralectotypes.

Lectotype Measurements. Length 25.9 mm, diameter (excluding lip) 10.3 mm; aperture height (including lip) 9.6 mm, aperture width (including lip and peristome) 7.7 mm.

Type Locality. Found in vicinity of well at extreme south end of [Great Guana] Key [Exuma Group, Bahamas].

Remarks. Maynard and Clapp *in* Maynard (1920d: 118) erred in citing the wrong illustrations in their original description. The illustrations were correctly captioned and published at the same time as the description. Clench (1957: 145) corrected this error. Maynard (1920d: 118) reported that all 150 specimens were collected dead and were of about the same age as *Strophiops prognata,* with some specimens showing reddish markings. Maynard (1924: 173) added ecological information and confirmed that 150 specimens were collected.

Taxon 146. *Strophiops imperfecta* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 118–119, pl. 1** [sic, actually 3], **figs. 1, 2, map 1, 10.** Examined two specimens. Size given as 1.05 by .40 [inches; 26.7 by 10.2 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the two specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in the original description or in any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on two syntypes. Of these, MCZ 76313, which was labeled "Holotype" and contains a single specimen accompanied by a note in Maynard's handwriting with the term "type" is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The other syntype become a paralectotype.

Lectotype Measurements. Length 27.7 mm, diameter (excluding lip) 11.6 mm; aperture height (including lip) 10.4 mm, aperture width (including lip and peristome) 9.8 mm.

Type Locality. Near well, on south end of Great Guana Key [Exuma Group, Bahamas].

Remarks. Maynard and Clapp *in* Maynard (1920d: 118) erred in citing the wrong plate number but the correct figure numbers in their description of this taxon. The illustrations were correctly captioned and published at the same time as the description. Clench (1957: 148) corrected this error. Maynard (1920d: 119) reported this taxon to be fossil, embedded in rock.

Taxon 147. *Strophiops progressa* Maynard, 1919b [November 6]: 32, 34, 35 [nonem nudum]; **Maynard and Clapp *in* Maynard, 1920d [September 30]: 119, pl. 2, figs. 1–3.** Examined 1,738 specimens. Size given as 1.15 by .45 [inches; 29.2 by 11.4 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 1,738 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that

types were selected. However, there was no indication in the original description or in any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 1,738 syntypes. Lot MCZ 76197 contains a single specimen labeled "Holotype" that approximates the measurements and illustration of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 1,737 syntypes, including MCZ 118179 and USNM 419947 (100 specimens), become paralectotypes.

Lectotype Measurements. Length 29.6 mm, diameter (excluding lip) 12.1 mm; aperture height (including lip) 11.4 mm, aperture width (including lip and peristome) 10.0 mm.

Type Locality. Near Black Point, north end of Great Guana Key [Exuma Group, Bahamas].

Remarks. This binomen appeared as a nomen nudum (Maynard, 1919b: 32, 34, 35) before its description.

Taxon 148. *Strophiops cyclura* Maynard, 1919a [October 16]: 24 [nomen nudum]; Maynard, 1919b [November 6]: 25 [nomen nudum]; **Maynard and Clapp *in* Maynard, 1920d [September 30]: 119, pl. 3, figs. 3–5**; Maynard, 1925: 181–185. Examined 4,422 specimens. Size given as 1.10 by .40 [inches; 27.9 by 10.2 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 4,422 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in the original description or in any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon and the species is based on 4,422 syntypes. Lot MCZ 76045 contains a single specimen labeled "Holotype" that approximates the measurements and illustration of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 4,421 syntypes, including MCZ 76046, MCZ 118235, and USNM 419949 (500 specimens), become paralectotypes.

Lectotype Measurements. Length 28.8 mm, diameter (excluding lip) 11.6 mm; aperture height (including lip) 10.3 mm, aperture width (including lip and peristome) 8.9 mm.

Type Locality. Bitter Guana [Key, Exuma Group, Bahamas].

Remarks. This binomen first appeared as a nomen nudum (Maynard, 1919a: 24, 1919b: 25). Maynard (1925: 181–185) provided additional anatomical information on this taxon and noted that he collected 82 specimens from a single lily plant.

Taxon 149. *Strophiops dissimila* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 119, pl. 24, figs. 8, 9.** Examined 86 specimens. Measurements not provided.

Type Material. The original description did not distinguish among the 86 specimens examined. Maynard (1926: 195) reported that 275 specimens were collected. Presumably 189 of these specimens were collected after the taxon was described. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in the original description or in any of Maynard's publications to associate a single specimen

with the term "type." Thus, there is no holotype for this taxon, and the species is based on 86 syntypes. Of these, MCZ 76057, which was labeled "Holotype" and contains a single specimen accompanied by a note in Maynard's handwriting identifying the taxon but not using the term "type," is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 85 syntypes, which might have been co-mingled with 189 subsequently collected non-type specimens, become paralectotypes.

Lectotype Measurements. Length 29.4 mm, diameter (excluding lip) 11.7 mm; aperture height (including lip) 11.2 mm, aperture width (including lip and peristome) 8.9 mm.

Type Locality. East Cistern Key [Exuma Group, Bahamas].

Remarks. Maynard (1920d: 119) reported this taxon to occur on palm fronds and bushes.

Taxon 150. *Strophiops veta* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 120, pl. 21, figs. 3, 4.** Examined 80 specimens. Size given as 1.25 by .50 [inches; 31.8 by 12.7 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 80 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in the original description or in any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 80 syntypes. Lot MCZ 76221 contains a single specimen labeled "Holotype" that approximates the illustration and the measurements of this taxon and is accompanied by a label in Maynard's hand with the term "type" that includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 79 syntypes become paralectotypes.

Lectotype Measurements. Length 31.4 mm, diameter (excluding lip) 12.2 mm; aperture height (including lip) 11.5 mm, aperture width (including lip and peristome) 8.9 mm.

Type Locality. Strout's [Stroud's] Key [Exuma Group, Bahamas]. Fossil in cliff on west side.

Remarks. Maynard (1920d: 120) reported this taxon to be the immediate ancestor of *S. stroutii.*

Taxon 151. *Strophiops stroutii* Maynard, 1919a [October 16]: 15 [nomen nudum]; Maynard, 1919b [November 6]: 35 [nomen nudum]; **Maynard and Clapp *in* Maynard, 1920d [September 30]: 120, pl. 21, figs. 1, 2**; Maynard, 1926: 198–203. Examined 1,951 specimens. Measurements not provided.

Type Material. The original description did not distinguish among the 1,951 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in the original description or in any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 1,951 syntypes. Lot MCZ 76130 contains a single specimen labeled "Holotype" that approximates the illustration of this taxon [no measurements were published] and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 1,951 syntypes, including MCZ

76131, MCZ 76132, MCZ 118195, USNM 420000 (200 specimens), and USNM 420122 (200 specimens), become paralectotypes.

Lectotype Measurements. Length 30.3 mm, diameter (excluding lip) 12.2 mm; aperture height (including lip) 10.3 mm, aperture width (including lip and peristome) 8.3 mm.

Type Locality. Maynard (1920d: 120) and Clench (1957: 164) listed this taxon as occurring on Little Strout [Stroud], Strout [Stroud], East and West Hawksbill and Cistern Keys [Exuma Group, Bahamas]. The lectotype is from Strout [Stroud] Key.

Remarks. Maynard (1919a: 15, 1919b: 35) twice introduced this binomen as a nomen nudum. Maynard (1926: 198–203) provided additional data on the basis of dissections and noted that this was one of a very few taxa that occurred on more than a single key.

Taxon 152. *Strophiops palmata minuta* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 120, pl. 21, fig. 5.** Examined 600 specimens. Size given as .95 by .40 [inches; 24.13 by 10.2 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 600 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in the original description or in any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 600 syntypes. Because no specimen labeled "Holotype" or accompanied by a label in Maynard's hand could be found, a specimen, USNM 420093, that most closely approximates the published measurements and figure is here designated as lectotype from a large syntype lot at USNM to provide an objective standard of reference for this species-group taxon. The remaining 599 syntypes, including MCZ 76214, MCZ 118243, and USNM 1093792, become paralectotypes.

Lectotype Measurements. Length 24.2 mm, diameter (excluding lip) 9.9 mm; aperture height (including lip) 8.6 mm, aperture width (including lip and peristome) 7.4 mm.

Type Locality. Wax Key [Great Exuma Island, Exuma Cays, Bahamas].

Remarks. Maynard (1926: 213–218) provided additional data on shell morphology and anatomy.

Taxon 153. *Strophiops degenis* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 120–121, pl. 4, figs. 6, 7.** Examined 34 specimens. Size given as 1.10 by .45 [inches; 27.9 by 11.4 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 34 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in the original description or in any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 34 syntypes. Lot MCZ 76404 contains a single specimen labeled "Holotype" that approx-

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Figures 151–162. Taxon 151. *Strophiops stroutii* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76130. Strout [Stroud], Key, Exuma Group, Bahamas. Taxon 152. *Strophiops palmata minuta* Maynard and Clapp *in* Maynard, 1920. Lectotype USNM 420093. Wax Key, Great Exuma Island, Exuma Cays, Bahamas. Taxon 153. *Strophiops degenis* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76404. Harvest Key, Harvey Cay, Exuma Cays, Bahamas. Taxon 154. *Strophiops sampsoni* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76235. North beach of Sampson's Key, Exuma Cays, Bahamas. Taxon 155. *Strophiops tenucostata* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76194. South Beach of Sampson's Key, Exuma Cays, Bahamas. Taxon 156. *Strophiops fulvia* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76159. East side of Pipe Key, Exuma Group, Bahamas. Taxon 157. *Strophiops inquita* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76182. Fowl

Key, Exuma Group, Bahamas. Taxon 158. *Strophiops cervina* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76047. Refuge Key, east of Norman's Pond Key, Exuma Cays, Bahamas. Taxon 159. *Strophiops pulla* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76217. Key opposite Roseville, Great Exuma, Exuma Cays, Bahamas. Taxon 160. *Strophiops caerulescens* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76198. Key north of key opposite Roseville, Great Exuma, Bahamas. Taxon 161. *Strophiops nebula* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76039. First key north of Stocking Island, Exuma Cays, Bahamas. Taxon 162. *Strophiops exorta* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76405. Interior of Refuge Key, Exuma Group, Bahamas.

imates the illustration and the measurements of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 33 syntypes become paralectotypes.

Lectotype Measurements. Length 28.0 mm, diameter (excluding lip) 11.1 mm; aperture height (including lip) 9.4 mm, aperture width (including lip and peristome) 7.6 mm.

Type Locality. Harvest Key [Harvey Cay, Exuma Cays, Bahamas].

Remarks. Maynard (1920d: 121) reported this taxon as occurring very scattered on palms, bushes, and rocks.

Taxon 154. *Strophiops sampsoni* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 121, pl. 4, figs. 1, 10.** Examined 1,540 specimens. Size given as 1.20 by .50 [inches; 30.5 by 12.7 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 1,540 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 1,540 syntypes. Lot MCZ 76235 was labeled "Holotype" but contains two syntypes, one of which matches closely the published dimensions and illustration of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The other specimen has been recatalogued as MCZ 357004. The remaining 1,539 syntypes, including MCZ 357004, MCZ 76236, MCZ 118237, and USNM 420090 (100 specimens), become paralectotypes.

Lectotype Measurements. Length 30.4 mm, diameter (excluding lip) 11.6 mm; aperture height (including lip) 10.4 mm, aperture width (including lip and peristome) 8.4 mm.

Type Locality. North beach of Sampson's Key [Exuma Cays, Bahamas].

Remarks. Maynard (1920d: 121) reported this taxon was common on palms.

Taxon 155. *Strophiops tenucostata* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 121, pl. 4, figs. 3** [sic, actually 8], **9.** Examined 112 specimens. Measurements not provided.

Type Material. The original description did not distinguish among the 112 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 112 syntypes. Lot MCZ 76194 contains a single specimen labeled "Holotype" that matches the illustrations of this taxon and is accompanied by a label in Maynard's hand with the term "type." This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 111 syntypes, including MCZ 76195, become paralectotypes.

Lectotype Measurements. Length 28.5 mm, diameter (excluding lip) 11.0 mm; aperture height (including lip) 9.9 mm, aperture width (including lip and peristome) 7.9 mm.

Type Locality. South Beach of Sampson's Key [Exuma Cays, Bahamas].

Remarks. Maynard (1920d: 121) reported this occurred on palms but was not very common.

Taxon 156. *Strophiops fulvia* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 121, pl. 4, figs. 4, 5.** Number of specimens examined not given. Size given as 1.15 by .40 [inches; 29.2 by 10.2 mm], but the term "type" was not used.

Type Material. The original description did not specify the number of specimens examined but noted that they were common. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on an undetermined number of syntypes. Lot MCZ 76159 contains a single specimen labeled "Holotype" that matches closely the published dimensions and illustration of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining syntypes, including MCZ 76158, MCZ 118223, and USNM 420039 (100 specimens), become paralectotypes.

Lectotype Measurements. Length 29.5 mm, diameter (excluding lip) 11.4 mm; aperture height (including lip) 9.9 mm, aperture width (including lip and peristome) 7.6 mm.

Type Locality. On the east side of Pipe Key [Exuma Group, Bahamas].

Remarks. Maynard (1920d: 121) reported this taxon to be common beneath palm fronds.

Taxon 157. *Strophiops inquita* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 121, pl. 4, figs. 2, 3** [figure caption as *S. inquieta*]. Neither the number of specimens nor the measurements are provided.

Type Material. The original description did not distinguish among the unspecified number of specimens examined but noted that this taxon was found in 11 small, isolated groups, indicating, at a minimum, 11 syntypes. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 11 or more syntypes. Lot MCZ 76182 contains 14 adult specimens and a juvenile and was labeled "Paratype." No labels by Maynard accompany this lot. The specimen that most closely resembles the illustrations in size and proportion and in the visibility of a weak columellar tooth is selected as lectotype. The remaining 13 adults and juvenile, recatalogued as MCZ 357005, are paralectotypes.

Lectotype Measurements. Length 30.6 mm, diameter (excluding lip) 12.4 mm; aperture height (including lip) 10.8 mm, aperture width (including lip and peristome) 9.1 mm.

Type Locality. Fowl Key [Exuma Group, Bahamas].

Remarks. The taxon name originally appeared as *Strophiops inquita* in the heading of the original description, but as *S. inquieta* in the caption to the figures in the plate. The spellings *inquita* and *inquieta* are thus different original spellings. Maynard never referred to this taxon again, and it was not listed in his catalog. Clench (1957: 149) listed this taxon as *inquita,* but cannot be considered the First Revisor [Article 24.2.3, ICZN, 1999: 30] because he did not list both original spellings. *Strophiops inquita* is here formally selected as the correct original spelling. Maynard (1920d: 121) reported that this taxon was

nearly exterminated by cultivation when he encountered it in 1915.

Taxon 158. *Strophiops cervina* Maynard, 1919a [October 16]: 21 [nomen nudum]; **Maynard and Clapp *in* Maynard, 1920d [September 30]: 121, pl. 22, figs. 8, 9.** Examined 3,480 specimens. Size given as 1.30 by .47 [inches; 33.0 by 11.9 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 3,480 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 3,480 syntypes. Perusal of the MCZ catalog indicated that no specimen identified by Maynard as "type" could be recognized in his collection when it reached MCZ. Lot MCZ 76047 comprised 158 specimens that were labeled "paratypes." Segregated in a vial were two specimens, a juvenile and a transversely broken adult shell, together with a label referring to "fig. 124a," which was never published. A specimen matching the published measurements and approximating the illustrations was selected as lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 157 specimens were recatalogued as MCZ 357006. These and MCZ 118251 and USNM 419938 are among the 3,479 syntypes that become paralectotypes.

Lectotype Measurements. Length 33.0 mm, diameter (excluding lip) 11.9 mm; aperture height (including lip) 11.1 mm, aperture width (including lip and peristome) 8.6 mm.

Type Locality. Refuge Key (east of Norman's Pond Key) [Exuma Cays, Bahamas].

Remarks. Maynard's (1919a: 21) first use of this binomen was a nomen nudum. Later (1920d: 121), he reported this taxon to be exceedingly abundant on palms, bushes, and small trees.

Taxon 159. *Strophiops pulla* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 122, pl. 23, figs. 3, 4.** Examined 1,572 specimens. Size given as 1.05 by .45 [inches; 26.7 by 11.4 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 1,572 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 1,572 syntypes. Lot MCZ 76217 contains a single specimen labeled "Holotype" that approximates the measurements and illustration of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 1,571 syntypes, including MCZ 76218 and USNM 419948 (100 specimens), become paralectotypes.

Lectotype Measurements. Length 26.6 mm, diameter (excluding lip) 12.0 mm; aperture height (including lip) 9.8 mm, aperture width (including lip and peristome) 8.2 mm.

Type Locality. Key opposite Roseville, Great Exuma, Exuma Cays, Bahamas.

Remarks. Maynard (1920d: 122) reported this taxon to be common on bushes.

Taxon 160. *Strophiops caerulescens* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 122, pl. 22, fig. 10, pl. 23, fig. 5.** Examined 2,000 speci-

mens. Size given as 1.30 by .50 [inches; 33.0 by 12.7 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 2,000 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 2,000 syntypes. Lot MCZ 76198 contains a single specimen labeled "Holotype" that approximates the measurements and illustration of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 1,999 syntypes, including MCZ 76199, MCZ 118268, MCZ 357007 and USNM 419965 (300 specimens), become paralectotypes.

Lectotype Measurements. Length 33.0 mm, diameter (excluding lip) 13.3 mm; aperture height (including lip) 11.4 mm, aperture width (including lip and peristome) 10.0 mm.

Type Locality. Key north of key opposite Roseville, Great Exuma, Bahamas.

Remarks. Maynard (1920d: 122) reported this taxon to be common, chiefly on palms. Clench (1934: 214) noted that he compared specimens from Strachan, Saltwater Pond, and Clem Cays off Clarencetown, Long Island, with the type specimen of *Cerion caerulescens* from Exuma and thought the differences to be only colonial.

Taxon 161. *Strophiops nebula* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 122, pl. 23, fig. 10, pl. 24, fig. 1.** Examined 250 specimens. Size given as 1.20 by .44 [inches; 30.5 by 11.2 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 250 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 250 syntypes. Of these, MCZ 76039, which was labeled "Holotype" and contains a single specimen accompanied by a note in Maynard's handwriting with the term "type," is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 249 syntypes become paralectotypes.

Lectotype Measurements. Length 28.7 mm, diameter (excluding lip) 11.5 mm; aperture height (including lip) 10.8 mm, aperture width (including lip and peristome) 9.3 mm.

Type Locality. First key north of Stocking Island, Exuma Cays, Bahamas.

Remarks. Maynard (1920d: 122) reported this taxon to be rather uncommon on palms.

Taxon 162. *Strophiops exorta* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 122, pl. 24, figs. 4, 5.** Examined nine specimens. Size given as .90 by .35 [inches; 22.9 by 8.9 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the nine specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is

based on nine syntypes. Lot MCZ 76405 contains a single specimen labeled "Holotype" that approximates the illustration and the measurements of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining eight syntypes become paralectotypes.

Lectotype Measurements. Length 23.1 mm, diameter (excluding lip) 10.0 mm; aperture height (including lip) 8.8 mm, aperture width (including lip and peristome) 7.8 mm.

Type Locality. Interior of Refuge Key, Exuma Group, Bahamas.

Remarks. Maynard (1920d: 122) reported this taxon to be limited to a small colony of nine specimens.

Taxon 163. *Strophiops cylindriata* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 123, pl. 23, figs. 8, 9.** Examined 132 specimens. Size given as 1.35 by .50 [inches; 34.3 by 12.7 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 132 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 132 syntypes. Of these, MCZ 76031, which was labeled "Holotype" and contains a single specimen accompanied by a note in Maynard's handwriting with the term "type," is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 131 syntypes become paralectotypes.

Lectotype Measurements. Length 33.4 mm, diameter (excluding lip) 13.3 mm; aperture height (including lip) 11.4 mm, aperture width (including lip and peristome) 9.23 mm.

Type Locality. First key north of Leward Stocking Key, Exuma Group, Bahamas.

Remarks. Maynard (1920d: 123) reported this taxon to occur beneath palm fronds.

Taxon 164. *Strophiops exasperata* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 123, pl. 23, figs. 1, 2.** Examined 572 specimens. Size given as 1.27 by .47 [inches; 32.3 by 11.9 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 572 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 572 syntypes. Lot MCZ 76041 contains a single specimen labeled "Holotype" that approximates the illustration

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Figures 163–174. Taxon 163. *Strophiops cylindriata* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76031. First key north of Leward Stocking Key, Exuma Group, Bahamas. Taxon 164. *Strophiops exasperata* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76041. Northeast point, Key east of Anna's Tract, Great Exuma, Bahamas. Taxon 165. *Strophiops crassa* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76220. East Hill, Little Norman's Key, Exuma Cays, Bahamas. Taxon 166. *Strophiops normanii* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76248. West Hill, Little Norman's Key, Exuma Group, Bahamas. Taxon 167. *Strophiops semipolita* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76033. Third key southeast of Roseville, Great Exuma, Bahamas. Taxon 168. *Strophiops accuminator* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76349. Long Key, Long Cay, Exuma Group, Bahamas. Taxon 169. *Strophiops navalis* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76035. South end of Ship Channel Key, Exuma Group, Bahamas. Taxon 170. *Strophiops valida*

Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76043. Near well on west coast of Ship Channel Key, Exuma Group, Bahamas. Taxon 171. *Strophiops genetiva* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76037. On south end of Ship Channel Key, Exuma Group, Bahamas. Taxon 172. *Strophiops marmorosa* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76185. Well Key, a little north of Leward Stocking Key, Exuma Group, Bahamas. Taxon 173. *Strophiops pusilla* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76053. Key near Long Rock, Great Exuma, Exuma Group, Bahamas. Taxon 174. *Strophiops inexpecta* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76307. Fossil in soft rock next to westernmost Brigadier Key, Exuma Group, Bahamas.

and the measurements of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 571 syntypes, including MCZ 76042, MCZ 118234, and USNM 420006 (75 specimens), become paralectotypes.

Lectotype Measurements. Length 32.7 mm, diameter (excluding lip) 12.5 mm; aperture height (including lip) 11.3 mm, aperture width (including lip and peristome) 8.6 mm.

Type Locality. Northeast point, key east of Anna's Tract, Great Exuma, Bahamas.

Remarks. Maynard (1920d: 123) reported this taxon to occur in a small area on shrubs.

Taxon 165. *Strophiops crassa* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 123, pl. 21, figs. 9, 10.** Examined 400 specimens. Size given as 1.37 by .50 [inches; 34.8 by 12.7 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 400 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 400 syntypes. Lot MCZ 76220 contains a single specimen labeled "Holotype" that approximates the illustration and the measurements of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 399 syntypes, including MCZ 76219 and USNM 420007 (100 specimens), become paralectotypes.

Lectotype Measurements. Length 32.3 mm, diameter (excluding lip) 12.8 mm; aperture height (including lip) 11.4 mm, aperture width (including lip and peristome) 9.6 mm.

Type Locality. East Hill, Little Norman's Key, Exuma Cays, Bahamas.

Remarks. Maynard (1920d: 123) reported this taxon to occur not very commonly at the base of shrubbery.

Taxon 166. *Strophiops normanii* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 123, pl. 21, fig. 8, pl. 20, fig. 5** [as *normandi*]. Examined 400 specimens. Size given as 1.25 by .38 [inches; 31.8 by 9.7 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 400 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 400 syntypes. Lot MCZ 76248 contains a single specimen labeled "Holotype" that approximates the measurements and illustration of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 399 syntypes, including MCZ 76249 and USNM 420094 (100 specimens), become paralectotypes.

Lectotype Measurements. Length 31.3 mm, diameter (excluding lip) 12.7 mm; aperture height (including lip) 11.5 mm, ap-

erture width (including lip and peristome) 9.1 mm.

Type Locality. West Hill, Little Norman's Key, Exuma Group, Bahamas.

Remarks. The taxon name originally appeared as *Strophiops normanii* in the heading of the original description, but as *S. normandi* in the caption to the figures in the plate. The spellings *normanii* and *normandi* are thus different original spellings. Maynard never referred to this taxon again, and it was not listed in his catalog. Clench (1957: 155) listed this taxon as *normanii,* but cannot be considered the First Revisor [Article 24.2.3, ICZN, 1999: 30] because he did not list both original spellings. *Strophiops normanii* is here formally selected as the correct original spelling. Maynard (1920d: 123) reported this taxon to occur on the ground, with few living and many dead specimens.

Taxon 167. *Strophiops semipolita* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 123, pl. 23, figs. 6, 7.** Examined 385 specimens. Size given as 1.30 by .50 [inches; 33.0 by 12.7 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 385 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 385 syntypes. Lot MCZ 76033 contains a single specimen labeled "Holotype" that approximates the illustration and the measurements of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to subsequently published figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 384 syntypes, including MCZ 76034 and MCZ 118254, become paralectotypes.

Lectotype Measurements. Length 34.2 mm, diameter (excluding lip) 14.0 mm; aperture height (including lip) 11.7 mm, aperture width (including lip and peristome) 9.7 mm.

Type Locality. Third key southeast of Roseville, Great Exuma, Bahamas.

Taxon 168. *Strophiops acuminata* Maynard, 1920b [April 8]: 84 [nomen nudum]. *Strophiops accuminator* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 124, pl. 3, fig. 6** [juvenile specimens], **pl. 20, figs. 1, 2** [*S. accumulata* on pl. 20]. Examined 1,500 specimens. Size given as 1.15 by .47 [inches; 29.2 by 11.9 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 1,500 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 1,500 syntypes. Lot MCZ 76349 contains a single specimen labeled "Holotype" that approximates the measurements and illustration of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 1,499 syntypes, including MCZ 76348 and USNM 420062 (100 specimens), become paralectotypes.

Lectotype Measurements. Length 29.0 mm, diameter (excluding lip) 11.5 mm; aperture height (including lip) 9.7 mm, ap-

erture width (including lip and peristome) 7.4 mm.

Type Locality. Long Key [Long Cay, Exuma Group, Bahamas].

Remarks. The taxon name *Strophiops acuminata* first appeared as a nomen nudum (Maynard, 1920b [April 8]: 84). The next to appear was *S. accuminator* in the heading of the original description, but as *S. accumulata* in the caption to the figures in one of two plates. The spellings *accuminator* and *accumulata* are thus different original spellings. Maynard (1924b?: [3]) listed the taxon as *acuminator* [one *c*] in his catalog. Clench (1957: 136) listed this taxon as *accuminator,* but cannot be considered the First Revisor [Article 24.2.3, ICZN, 1999: 30] because he did not list both original spellings. *Strophiops accuminator* is here formally selected as the correct original spelling.

Taxon 169. *Strophiops navalia* Maynard, 1919b [November 6]: 32 [nomen nudum]; Maynard, 1919b [November 6]: 35 [nomen nudum]. *Strophiops navalis* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 124, pl. 20, figs. 8–10.** Examined 1,070 specimens. Size given as 1.25 by .50 [inches; 31.8 by 12.7 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 1,070 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 1,070 syntypes. Lot MCZ 76035 contains a single specimen labeled "Holotype" that approximates the measurements and illustration of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 1,069 syntypes, including MCZ 76036, MCZ 118226, and USNM 420015 (50 specimens), become paralectotypes.

Lectotype Measurements. Length 30.9 mm, diameter (excluding lip) 12.3 mm; aperture height (including lip) 11.4 mm, aperture width (including lip and peristome) 9.2 mm.

Type Locality. South end of Ship Channel Key [Exuma Group, Bahamas].

Remarks. The binomen *S. navalia* appeared twice as a nomen nudum (Maynard, 1919b [November 6]: 32, 35).

Taxon 170. *Strophiops valida* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 124, pl. 22, figs. 1, 2.** Examined 400 specimens. Size given as 1.20 by .55 [inches; 30.5 by 14.0 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 400 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 400 syntypes. MCZ 76043 contains a single specimen labeled "Holotype" that approximates the measurements and the illustration for this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 399 syntypes, including MCZ 76044, become paralectotypes.

Lectotype Measurements. Length 30.3

mm, diameter (excluding lip) 14.1 mm; aperture height (including lip) 11.9 mm, aperture width (including lip and peristome) 10.4 mm.

Type Locality. Near well on west coast of Ship Channel Key [Exuma Group, Bahamas].

Remarks. Because *Strophiops* is considered to be a subgenus of *Cerion* in current classifications, *Strophiops valida* Maynard and Clapp *in* Maynard, 1920, is a junior secondary homonym of *Cerion* (*Maynardia*) *columna* var. *valida* Pilsbry and Vanatta, 1895. In our view, it is likely that future research will identify a synonym for *Strophiops valida* Maynard and Clapp *in* Maynard, 1920 [Article 60.2, ICZN, 1999: 62], and that establishing a replacement name would only create an additional synonym.

Taxon 171. *Strophiops genitiva* Maynard, 1919b [November 6]: 32, 35 [nomen nudum]. *Strophiops genetiva* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 124** [*genitiva* in text], **pl. 22, figs. 3, 4** [*genetiva* on plate]. Examined 400 specimens. Size given as 1.50 by .60 [inches; 38.1 by 15.2 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 400 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 400 syntypes. Lot MCZ 76037 contains a single specimen labeled "Holotype" that approximates the illustrations and measurements of this taxon. This specimen is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 399 syntypes become paralectotypes.

Lectotype Measurements. Length 38.6 mm, diameter (excluding lip) 14.5 mm; aperture height (including lip) 12.3 mm, aperture width (including lip and peristome) 10.0 mm.

Type Locality. On south end of Ship Channel Key [Exuma Group, Bahamas].

Remarks. The binomen *S. genitiva* first appeared as a nomen nudum (Maynard, 1919b [November 6]: 32, 35). The taxon name was spelled *genitiva* in the original description and *genetiva* on the plate caption, which was published together with the text; thus, both names are different original spellings. Maynard (1924b?: [7]) listed the taxon as *genetiva* in his catalog, thus serving as the First Revisor of spellings [Article 24.2.4, ICZN, 1999: 30–31] and fixing the spelling as *genetiva*. Clench (1957: 146) listed this species as *genitiva*.

Taxon 172. *Strophiops marmorosa* **Maynard and Clapp *in* Maynard, 1920d [September 30]: 125, pl. 24, figs. 6, 7.** Unspecified number of specimens examined. Size given as 1.30 by .47 [inches; 33.0 by 11.9 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the unspecified number of specimens examined, but noted that this taxon was not common. The taxon is listed for sale in Maynard's (1924b?: [6]) catalog, indicating that more than one specimen was at hand. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on an uncertain number of syntypes. Lot MCZ 76185 contains a single specimen labeled "Holotype" that approximates

the measurements and the illustration for this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining syntypes, including MCZ 76184, MCZ 118242, and USNM 419944 (25 specimens), become paralectotypes.

Lectotype Measurements. Length 31.8 mm, diameter (excluding lip) 12.4 mm; aperture height (including lip) 10.6 mm, aperture width (including lip and peristome) 8.1 mm.

Type Locality. Well Key, a little north of Leward Stocking Key [Exuma Group, Bahamas].

Taxon 173. *Strophiops pusilla* **Maynard and Clapp *in* Maynard, 1920d [September 30], pl. 22, fig. 5**; Maynard and Clapp *in* Maynard, 1921a [May 2]: 127. Examined 700 specimens. Size given as .70 by .30 [inches; 17.8 by 7.6 mm], but the term "type" was not used.

Nomenclatural Remarks. The captioned illustration (Maynard 1920, pl. 25, fig. 5) was published before the text. The taxon thus dates from the publication of the name in the caption accompanying the illustrations, not from the subsequently published text (Article 12.2.7, ICZN, 1999: 17). The date of publication is September 30, 1920. Plate 22 was issued as part of "Part Two" of the *Contributions to the History of Cerionidae*; therefore, authorship of this taxon is attributed to Maynard and Clapp.

Type Material. Although the figure caption refers only to the single specimen illustrated, it is likely that the 700 specimens mentioned in the intended description of this taxon (Maynard and Clapp *in* Maynard, 1921a: 127) were available to Maynard at the time and are thus part of the type series [Article 72.4.1.1, ICZN, 1999: 76]. *Strophiops pusilla* is based on 700 syntypes. Lot MCZ 76053 contains a single specimen labeled "Holotype" that approximates the illustration more than the subsequently published measurements of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype. The remaining 699 specimens, including MCZ 76054 and USNM 420133, are paralectotypes.

Lectotype Measurements. Length 26.6 mm, diameter (excluding lip) 12.0 mm; aperture height (including lip) 9.8 mm, aperture width (including lip and peristome) 8.2 mm.

Type Locality. Key near Long Rock, Great Exuma [Exuma Group, Bahamas].

Remarks. Maynard (1921a: 127) reported that of 700 specimens examined, only 12 were living.

Taxon 174. *Strophiops inexpecta* **Maynard and Clapp *in* Maynard, 1920d [September 30], pl. 25, figs. 3, 4**; Maynard and Clapp *in* Maynard, 1921a [May 2]: 127. Unspecified number of specimens examined. Size given as 1.06 by .45 [inches; 29.9 by 11.4 mm], but the term "type" was not used.

Nomenclatural Remarks. The captioned illustrations (Maynard 1920, pl. 25, figs. 3, 4) were published before the text. The taxon thus dates from the publication of the name in the caption accompanying the illustrations, not from the subsequently published text (Article 12.2.7, ICZN, 1999: 17). The date of publication is September 30, 1920. Plate 25 was issued as part of "Part Two" of the *Contributions to the History of Cerionidae*; therefore, authorship of this taxon is attributed to Maynard and Clapp.

Type Material. There was no mention of other specimens in the plate caption, and the text portion published 7 months later did not specify the number of specimens that might have been available to Maynard

at the time the plate was prepared. The type series of *Strophiops inexpecta* likely consists of multiple specimens [Article 72.4.1.1, ICZN, 1999: 76], but the number is not known. There was no specimen labeled "Holotype" at the MCZ. Lot MCZ 76307 contains 9 specimens and was labeled "Paratypes." This lot contains a label in Maynard's hand that does not include the term "type" but does include references to the figures. Only one of these nine specimens is complete enough to match the illustration, although it does have some minor damage along the columella that is not represented in the figure. This specimen is the figured specimen and is here designated as the lectotype. The remaining specimens were recatalogued as MCZ 357008. These and MCZ 118187 are among the unspecified number of paralectotypes.

Lectotype Measurements. Length 27.1 mm, diameter (excluding lip) 12.0 mm; aperture height (including lip) 10.1 mm, aperture width (including lip and peristome) 8.9 mm.

Type Locality. Fossil in soft rock next to westernmost Brigadier Key [Exuma Group, Bahamas].

Taxon 175. *Strophiops fitzgeraldi* **Maynard and Clapp *in* Maynard, 1920d [September 30], pl. 25, figs. 6, 7**; Maynard and Clapp *in* Maynard, 1921a [May 2]: 127. Unspecified number of specimens examined. Size given as .85 by .37 [inches; 21.6 by 9.4 mm], but the term "type" was not used.

Nomenclatural Remarks. The captioned illustrations (Maynard 1920, pl. 25, figs. 6, 7) were published before the text. The taxon thus dates from the publication of the name in the caption accompanying the illustrations, not from the subsequently published text (Article 12.2.7, ICZN, 1999: 17). The date of publication is September 30, 1920. Plate 25 was issued as a part of "Part Two" of the *Contributions to the History of Cerionidae*; therefore, authorship of this taxon is attributed to Maynard and Clapp *in* Maynard.

Type Material. There was no mention of other specimens in the plate caption, and the text portion published 7 months later did not specify the number of specimens that might have been available to Maynard at the time the plate was prepared. The type series of *Strophiops fitzgeraldi* likely consists of multiple specimens [Article 72.4.1.1, ICZN, 1999: 76], but the number is not known. Lot MCZ 76051 contains a single specimen labeled "Holotype" that approximates the illustrations and is within a half millimeter of the subsequently published measurements of this taxon. This specimen, which is accompanied by a label in Maynard's hand with the term "type" that includes references to the figures, is here designated as the lectotype.

Lectotype Measurements. Length 22.4 mm, diameter (excluding lip) 9.9 mm; aperture height (including lip) 8.2 mm, aperture width (including lip and peristome) 7.7 mm.

Type Locality. North end of Little Exuma [Exuma Group, Bahamas], on the Fitzgerald Estate.

Taxon 176. *Strophiops adumbra* **Maynard and Clapp *in* Maynard, 1920d [September 30], pl. 25, figs. 10, 11**; Maynard, 1924c [10 December]: 2. Examined 79 specimens. Size given as .75 by .30 [inches; 19.1 by 7.6 mm], but the term "type" was not used.

Nomenclatural Remarks. The captioned illustrations (Maynard, 1920d, pl. 25, figs. 10–11) were published before the text. The taxon thus dates from the publication of the name in the caption accompanying the illustrations, not from the subsequently published text (Article 12.2.7, ICZN, 1999: 17). Plate 25 was published in "Part Two" of the *Contributions to the History of the Cerionidae*; therefore, the authorship of this taxon is attributed to Maynard and Clapp *in* Maynard.

Type Material. There was no mention of

other specimens in the plate caption, but it is likely that the 79 specimens referred to in the text portion published 7 months later were available to Maynard at the time the plate was prepared. The type series of *Strophiops adumbra* thus consists of 79 specimens [Article 72.4.1.1, ICZN, 1999: 76] that are syntypes. Lot MCZ 76029 contains a single specimen labeled "Holotype" that closely matches the illustrations and the subsequently published measurements of this taxon. This specimen is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is the figured specimen and is here designated as the lectotype. The remaining 78 specimens are paralectotypes.

Lectotype Measurements. Length 19.1 mm, diameter (excluding lip) 7.6 mm; aperture height (including lip) 7.2 mm, aperture width (including lip and peristome) 5.7 mm.

Type Locality. North side of a small key just south of Green Turtle Cut and north of Great Exuma.

Remarks. Maynard (1924c: 2) reported that all of the specimens were dead collected but that some were fresh.

Taxon 177. *Strophiops transmutata* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 127, pl. 26, figs. 1, 2** [figures labeled *S. transimutata*]. Examined 150 specimens. Size given as .95 by .35 [inches; 24.1 by 8.9 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 150 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 150 syntypes. Lot MCZ 76298 contains a single specimen labeled "Holotype" that approximates the illustration and the measurements of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 149 syntypes, including MCZ 76297 and MCZ 118183 (one specimen), become paralectotypes.

Lectotype Measurements. Length 22.6 mm, diameter (excluding lip) 8.9 mm; aperture height (including lip) 8.1 mm, aperture width (including lip and peristome) 6.4 mm.

Type Locality. Muddy Point Key, Great Exuma [Exuma Group, Bahamas].

Remarks. The taxon name appears as *transmutata* in the text and *transimutata* on the plate, both names were published on the same date and are different original spellings. Maynard (1924b?: [6]) listed this taxon as *transmutata,* acting as the First Revisor of spellings [Article 24.2.4, ICZN, 1999: 30–31]. Maynard (1921a: 127) reported that most of the specimens collected were dead.

Taxon 178. *Strophiops similaria* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 128, pl. 25, figs. 5, 6.** Examined

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Figures 175–186. Taxon 175. *Strophiops fitzgeraldi* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76051. North end of Little Exuma, Exuma Group, Bahamas, on the Fitzgerald Estate. Taxon 176. *Strophiops adumbra* Maynard and Clapp *in* Maynard, 1920. Lectotype MCZ 76029. North side of a small key just south of Green Turtle Cut and north of Great Exuma. Taxon 177. *Strophiops transmutata* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76298. Muddy Point Key, Great Exuma, Exuma Group, Bahamas. Taxon 178. *Strophiops similaria* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76055. Westernmost Brigadier Key, Great Exuma, Exuma Group, Bahamas. Taxon 179. *Strophiops flamea* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76155. Southwest Point of Great Exuma, Exuma Group, Bahamas. Taxon 180. *Strophiops proavita* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76143. Fossil in cliff at north end of Goat Key, Great Harbor,

Berry Islands, Bahamas. Taxon 181. *Strophiops intercalaria* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76160. Fossil in cliff at north end of Goat Key, Great Harbor, Berry Islands, Bahamas. Taxon 182. *Strophiops profunda* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76145. Fossil in cliff at north end of Goat Key, Great Harbor, Berry Islands, Bahamas. Taxon 183. *Strophiops mixta* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76175. Bonds Key, Berry Islands, Bahamas. Taxon 184. *Strophiops reliqua* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76206. Holmes' Key, Bahamas. Taxon 185. *Strophiops aviaria* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76171. Bird Key, Berry Islands, Bahamas. Taxon 186. *Strophiops confusa* Maynard and Clapp *in* Maynard, 1921. Lectotype USNM 420009. Little Harbor Key, Bahamas.

210 specimens. Original description states "size of last" [= *S. fragilis* = 1.00 by .40 (inches; 25.4 by 10.2 mm)].

Type Material. The original description did not distinguish among the 210 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 210 syntypes. Lot MCZ 76055 contains a single specimen labeled "Holotype" that approximates the illustration more than the measurements of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 209 syntypes, including MCZ 76056, become paralectotypes.

Lectotype Measurements. Length 25.8 mm, diameter (excluding lip) 9.8 mm; aperture height (including lip) 9.2 mm, aperture width (including lip and peristome) 7.5 mm.

Type Locality. Westernmost Brigadier Key, Great Exuma [Exuma Group, Bahamas].

Remarks. Maynard (1921a: 128) reported that most of the specimens collected were dead.

Taxon 179. *Strophiops flamea* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 128, pl. 25, figs. 8, 9.** Examined 340 specimens. Size given as 1.00 by .40 [inches; 25.4 by 10.2 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 340 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 340 syntypes. Lot MCZ 76155 contains a single specimen labeled "Holotype" that closely approximates the illustration and the measurements of this taxon. This specimen is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 339 syntypes, including MCZ 76156 and MCZ 118184 (one specimen), become paralectotypes.

Lectotype Measurements. Length 25.1 mm, diameter (excluding lip) 10.1 mm; aperture height (including lip) 9.3 mm, aperture width (including lip and peristome) 8.1 mm.

Type Locality. Southwest Point of Great Exuma [Exuma Group, Bahamas].

Remarks. Maynard (1921a: 128) reported that of 340 specimens, only 38 were living.

Taxon 180. *Strophiops proavita* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 129, pl. 26, figs. 9, 10.** Examined 40 specimens. Size given as 1.40 by .55 [inches; 35.6 by 14.0 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 40 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 40 syntypes. Lot MCZ 76143

contains a single specimen labeled "Holotype" that does not closely approximate either the illustrations or the measurements of this taxon. This specimen is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 39 syntypes, including MCZ 76144 and MCZ 118257, become paralectotypes.

Lectotype Measurements. Length 32.3 mm, diameter (excluding lip) 12.9 mm; aperture height (including lip) 12.1 mm, aperture width (including lip and peristome) 10.3 mm.

Type Locality. Fossil in cliff at north end of Goat Key, Great Harbor [Berry Islands, Bahamas].

Taxon 181. *Strophiops intercalaria* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 129, pl. 26, figs. 7, 9.** Examined 60 specimens. Size given as 1.30 by .50 [inches; 33.0 by 12.7 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 60 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 60 syntypes. Lot MCZ 76160 contains a single specimen labeled "Holotype" that approximates the illustration more than the measurements of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 59 syntypes, including MCZ 76161, become paralectotypes.

Lectotype Measurements. Length 35.8 mm, diameter (excluding lip) 14.5 mm; aperture height (including lip) 13.7 mm, aperture width (including lip and peristome) 11.3 mm.

Type Locality. Fossil in cliff at north end of Goat Key, Great Harbor [Berry Islands, Bahamas].

Taxon 182. *Strophiops profunda* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 129, pl. 27, figs. 1, 2.** Examined 115 specimens. Size given as 1.15 by .45 [inches; 29.2 by 11.4 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 115 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 115 syntypes. Lot number MCZ 76145 was labeled "paratype," contained two specimens, and was accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. Neither specimen matches closely the published measurements. The specimen that more closely approximates the illustrations is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The other specimen was recatalogued as MCZ 357009. It is one of the remaining 114 syntypes that become paralectotypes.

Lectotype Measurements. Length 32.0 mm, diameter (excluding lip) 11.7 mm; aperture height (including lip) 11.2 mm, aperture width (including lip and peristome) 9.4 mm.

Type Locality. Fossil in cliff at north end of Goat Key, Great Harbor [Berry Islands, Bahamas].

Taxon 183. *Strophiops mixta* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 130, pl. 27, figs. 5, 6.** Examined 1,005 specimens. Size given as 1.26 by .45 [inches; 32.0 by 11.4 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 1,005 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 1,005 syntypes. Lot MCZ 76175 contains a single specimen labeled "Holotype" that closely approximates the measurements and illustration of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 1,004 syntypes, including MCZ 76174, MCZ 118215, and USNM 420115 (100 specimens), become paralectotypes.

Lectotype Measurements. Length 32.0 mm, diameter (excluding lip) 12.2 mm; aperture height (including lip) 11.3 mm, aperture width (including lip and peristome) 10.1 mm.

Type Locality. Bonds Key [Berry Islands, Bahamas].

Remarks. Maynard (1921a: 130) reported that this taxon was common on palms.

Taxon 184. *Strophiops reliqua* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 130** [as *relequa* in text], **pl. 27, figs. 7, 8** [as *S. reliqua* on plate]. Examined 192 specimens. Size given as 1.16 by .40 [inches; 31.8 by 12.7 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 192 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 192 syntypes. Lot MCZ 76206 contains a single specimen labeled "Holotype" that approximates the illustration and the measurements of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 191 syntypes, including MCZ 76205, become paralectotypes.

Lectotype Measurements. Length 31.4 mm, diameter (excluding lip) 12.0 mm; aperture height (including lip) 11.4 mm, aperture width (including lip and peristome) 9.4 mm.

Type Locality. Holmes' Key [SW Grand Bahama Island, Bahamas].

Remarks. The taxon name appears as *relequa* in the text and *reliqua* on the plate, both published on the same date and both different original spellings. Maynard (1924b?: [7]) listed this taxon as *S. reliqua,* acting as the First Revisor of spellings [Article 24.2.4, ICZN, 1999: 30–31]. Clench (1957: 160) listed this taxon as *S. relequa.*

Taxon 185. *Strophiops aviaria* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 130, pl. 27, figs. 9, 10.** Examined 534 specimens. Size given as 1.16 by .40 [inches; 31.8 by 12.7 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 534 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 534 syntypes. Lot MCZ 76171 contains a single specimen labeled "Holotype" that closely approximates the measurements and illustration of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 533 syntypes, including MCZ 118206, MCZ 76170, and USNM 419942, become paralectotypes.

Lectotype Measurements. Length 28.2 mm, diameter 12.0 (excluding lip) mm; aperture height (including lip) 10.5 mm, aperture width (including lip and peristome) 8.6 mm.

Type Locality. Bird Key, Berry Islands, Bahamas.

Taxon 186. *Strophiops confusa* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 130, pl. 28, figs. 1, 2,** and 136, pl. 34, figs. 1, 2 [see Remarks]. Examined 1,272 specimens. Size given as 1.20 by .45 [inches; 30.5 by 11.4 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 1,272 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 1,272 syntypes. Lot MCZ 76324 contains three specimens and was labeled "Holotype." MCZ 118205 contains a single specimen and was labeled "paratype." None of these closely approximates the measurements or illustration of this taxon. A syntype, USNM 420009, that more closely matches the measurements in the original descriptions and conforms to the first illustration [pl. 28, figs. 1, 2] is here designated as the lectotype to provide an objective standard of reference for this species-group taxon. The remaining 1,271 syntypes, including MCZ 76168, MCZ 76324, MCZ 118205, and USNM 1093790, become paralectotypes.

Lectotype Measurements. Length 31.7 mm, diameter (excluding lip) 11.7 mm; aperture height (including lip) 11.3 mm, aperture width (including lip and peristome) 8.6 mm.

Type Locality. Little Harbor Key [Berry Islands, Bahamas].

Remarks. This taxon appears twice in the same publication: once on page 130 (pl. 28, figs. 1, 2), then again on page 136 (pl. 34, fig. 1, 2) [the second illustration appeared in the following issue dated July 15, 1921]. The descriptions differ (size, number of costae) but have the same type locality and list the same number of specimens examined. The figures are similar but do not represent the same specimen. The taxon originates from the first description (p. 130, pl. 28, figs. 1, 2). The second appearance of this taxon in the same issue is likely a lapsus on the part of Maynard. It is listed twice in the sales catalog (Maynard, 1924?: [3] nos. 63 [as *coufusa*] and 94, both from Little Harbor).

Taxon 187. *Strophiops candida* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 131, pl. 28, figs. 5, 6.** Examined 68 specimens. Size given as 1.25 by 0.50 [inches; 31.8 by 12.7 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 68 speci-

mens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 68 syntypes. Lot number MCZ 76151 contains a single specimen labeled "Holotype" that approximates the illustration and the measurements of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 67 syntypes, including MCZ 76152 and MCZ 118200, become paralectotypes.

Lectotype Measurements. Length 30.5 mm, diameter (excluding lip) 12.5 mm; aperture height (including lip) 11.6 mm, aperture width (including lip and peristome) 10.2 mm.

Type Locality. East Marketfish Key [Berry Islands, Bahamas].

Taxon 188. *Strophiops primordia* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 132, pl. 29, figs. 1, 2.** Examined 2,008 specimens. Size given as 1.35 by .50 [inches; 34.3 by 12.7 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 2,008 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 2,008 syntypes. Lot MCZ 76173 contains 179 syntypes [labeled "paratypes"], including a segregated specimen that approximates the figures and measurements listed in the original description. The segregated specimen is here selected as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's concept of this taxon. The remaining 178 specimens were recatalogued as MCZ 357010 and are among the 2,007 syntypes, including USNM 420126 (150 specimens), that become paralectotypes.

Lectotype Measurements. Length 33.7 mm, diameter (excluding lip) 12.9 mm; aperture height (including lip) 11.9 mm, aperture width (including lip and peristome) 10.2 mm.

Type Locality. Great Srirrup Key [Bahamas].

Taxon 189. *Strophiops balaena* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 132** [as *balaene*], **pl. 29, figs. 3, 4** [as *S. balaena*]. Examined 765 specimens. Size given as 1.20 by .40 [inches; 30.5 by 10.2 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 765 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's

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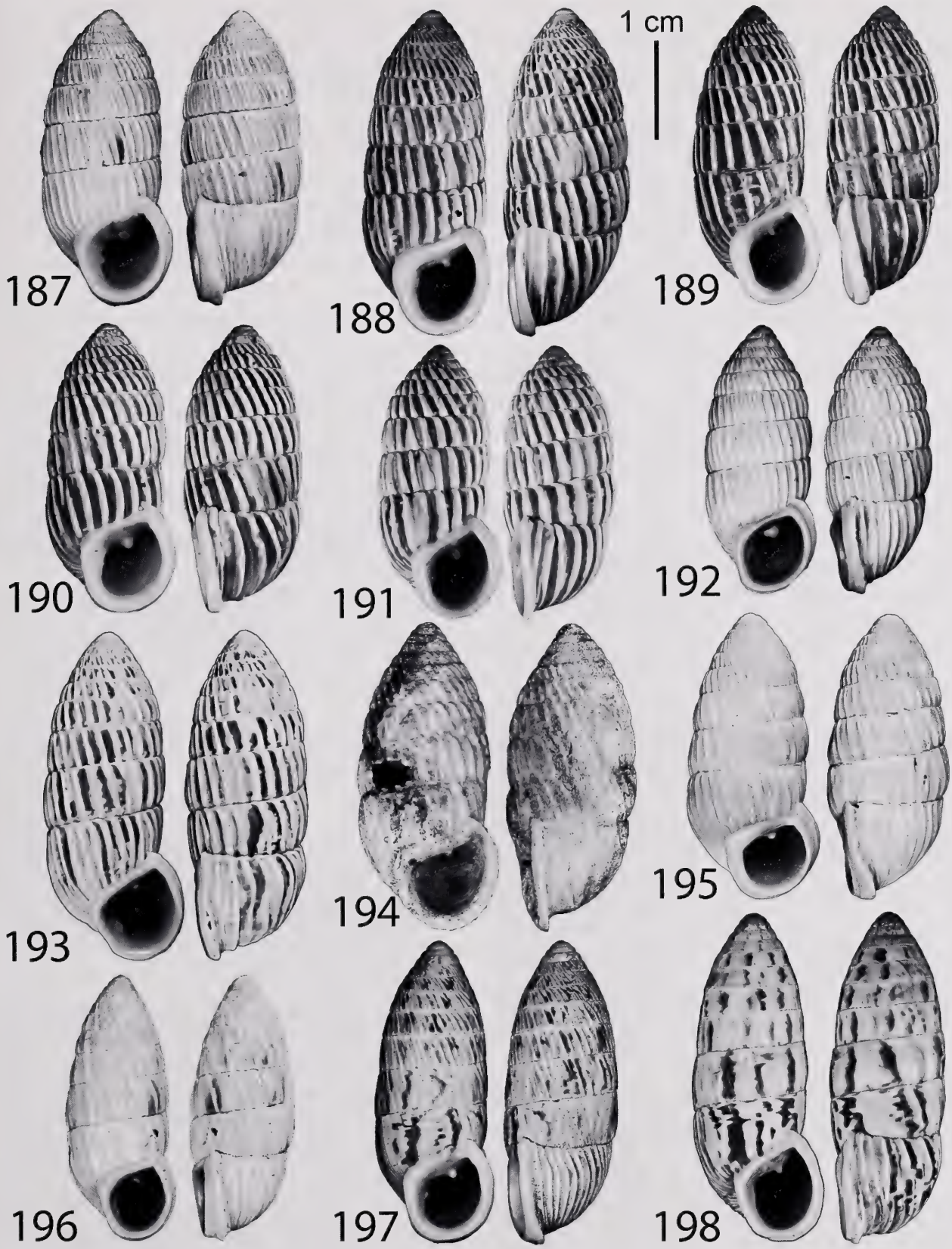
Figures 187–198. Taxon 187. *Strophiops candida* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76151. East Marketfish Key, Bahamas. Taxon 188. *Strophiops primordia* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76173. Great Srirrup Key, Bahamas. Taxon 189. *Strophiops balaena* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76190. Whale Key, Bahamas. Taxon 190. *Strophiops porcina* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76193 Frazar's Hog Key, Bahamas. Taxon 191. *Strophiops obtusa* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76213. Cat Key, Berry Islands, Bahamas. Taxon 192. *Strophiops albata* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76256. Hog Cay, 4 miles NW of Morgan's Bluff, Andros, Bahamas. Taxon 193. *Strophiops litorea* Maynard and Clapp *in* Maynard, 1921. Lectotype USNM



420058. South border of Guana Key, Berry Islands, Bahamas. Taxon 194. *Strophiops rara* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76023. West side of Cabbage Key, Bahamas. Taxon 195. *Strophiops scutata* Maynard and Clapp *in* Maynard, 1921. Lectotype USNM 420100. Petit Key, Berry Islands, Bahamas. Taxon 196. *Strophiops procliva* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76210. Goat Key, Great Harbor, Berry Islands, Bahamas. Taxon 197. *Strophiops jenneyi* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76012. Anderson's Key, Berry Islands, Bahamas. Taxon 198. *Strophiops travellii* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76363. Bridgewater Key, Berry Islands, Bahamas.

publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 765 syntypes. Lot number MCZ 76190 contains a single specimen labeled "Holotype" that approximates the illustration more than the measurements of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 764 syntypes, including MCZ 76191, MCZ 118213, and USNM 419943 (200 specimens), become paralectotypes.

Lectotype Measurements. Length 30.2 mm, diameter (excluding lip) 11.38 mm; aperture height (including lip) 11.4 mm, aperture width (including lip and peristome) 9.1 mm.

Type Locality. Whale Key [Berry Islands, Bahamas].

Remarks. The name of this taxon is spelled as *balaene* in the original description, *balaena* in the plate caption, and *balanae* in Maynard's (1924b?: [4]) sales catalog. The spellings *balaene* and *balaena* are different original spellings, whereas *balanae* is a subsequent lapsus calami. Clench (1957: 138) listed this taxon as *balaena* but cannot be considered the First Revisor [Article 24.2.3, ICZN, 1999: 30] because he did not list both original spellings. *Strophiops balaena* is here formally selected as the correct original spelling.

Taxon 190. *Strophiops porcina* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 132, pl. 29, figs. 7, 8.** Examined 2,305 specimens. Size given as 1.15 by .45 [inches; 29.2 by 11.4 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 2,305 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 2,305 syntypes. Lot number MCZ 76193 contains a single specimen labeled "Holotype" that approximates the illustration more than the measurements of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 2,304 syntypes, including MCZ 76192 and USNM 420012 (150 specimens), become paralectotypes.

Lectotype Measurements. Length 29.3 mm, diameter (excluding lip) 11.9 mm; aperture height (including lip) 11.4 mm, aperture width (including lip and peristome) 9.5 mm.

Type Locality. Frazar's Hog Key [Berry Islands, Bahamas].

Taxon 191. *Strophiops obtusa* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 132, pl. 29, figs. 9, 10.** Examined 1,500 specimens. Size given as 1.10 by .45 [inches; 27.9 by 11.4 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 1,500 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 1,500 syntypes. Lot MCZ 76213 contains a single specimen labeled "Holotype" that approximates the illustration more than the measurements of this taxon

and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 1,499 syntypes, including MCZ 76212, MCZ 118216, and USNM 420102 (500 specimens), become paralectotypes.

Lectotype Measurements. Length 28.1 mm, diameter (excluding lip) 11.2 mm; aperture height (including lip) 10.5 mm, aperture width (including lip and peristome) 9.1 mm.

Type Locality. Cat Key, Berry Islands, Bahamas.

Taxon 192. *Strophiops albata* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 132–133, pl. 30, figs. 3, 4.** Examined 60 specimens. Size given as 1.08 by .45 [inches; 30.5 by 11.4 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 60 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 60 syntypes. Lot number MCZ 76256 contains a single specimen labeled "Holotype" that approximates the illustration and less so the measurements of this taxon. It is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 59 syntypes, including MCZ 76257, become paralectotypes.

Lectotype Measurements. Length 27.8 mm, diameter (excluding lip) 11.1 mm; aperture height (including lip) 10.8 mm, aperture width (including lip and peristome) 8.9 mm.

Type Locality. "Hog Key near Morgan's Bluff." Clench (1957: 136) clarified the type locality as Hog Cay [4 miles NW of] Morgan's Bluff [Andros, Bahamas].

Remarks. See also *Strophiops albata* Maynard and Clapp *in* Maynard, 1921b [Taxon 215], and *Strophiops vagabunda* Maynard and Clapp *in* Maynard, 1925 [Taxon 248].

Taxon 193. *Strophiops litorea* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 133, pl. 30, figs. 7, 8.** Examined 500 specimens. Measurements not provided.

Type Material. The original description did not distinguish among the 500 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 500 syntypes. Lot number MCZ 76370 was labeled "holotype," but contains two specimens, neither of which closely match the published figure. A lectotype, USNM 420058, that more closely approximates the figure is here selected from a large syntype lot at USNM to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 499 syntypes, including MCZ 76369, MCZ 76370, and USNM 1093791, become paralectotypes.

Lectotype Measurements. Length 34.0 mm, diameter (excluding lip) 12.4 mm; aperture height (including lip) 11.1 mm, aperture width (including lip and peristome) 9.9 mm.

Type Locality. South border of Guana Key, Berry Islands, Bahamas.

Taxon 194. *Strophiops rara* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 133, pl. 31, figs. 1, 2.** Examined 10 specimens. Size given as 2.25 [sic, 1.25] by .52 [inches; 31.8 by 13.2 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 10 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 10 syntypes. Lot MCZ 76023 contains a single specimen labeled "Holotype" that approximates the illustration and the inferred measurements (see Remarks) of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining nine syntypes, including MCZ 76402 (one specimen), become paralectotypes.

Lectotype Measurements. Length 31.6 mm, diameter (excluding lip) 13.5 mm; aperture height (including lip) 11.6 mm, aperture width (including lip and peristome) 10.6 mm.

Type Locality. West side of Cabbage Key [Berry Islands], Bahamas.

Remarks. Fossil, embedded in rock. The length measurement provided, 2.25 inches, is likely a typographical error. The illustrated lectotype corresponds to a measurement of 1.25 inches.

Taxon 195. *Strophiops scutata* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 133–134, pl. 31, figs. 3, 4.** Examined 1,690 specimens. Size given as larger, 1.17 by .50 [inches; 30.5 by 12.7 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 1,690 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 1,690 syntypes. Of the specimens at the MCZ, none were found labeled "holotype," and only a single specimen (MCZ 118208) labeled "paratype" was located. A lectotype, USNM 420100, selected to most closely approximate the illustration and published measurements of this taxon, is here designated to provide an objective standard of reference for this species-group. The remaining 1,689 syntypes, including MCZ 76211, MCZ 118208, and USNM 1093793, become paralectotypes.

Lectotype Measurements. Length 29.4 mm, diameter (excluding lip) 12.7 mm; aperture height (including lip) 10.8 mm, aperture width (including lip and peristome) 9.8 mm.

Type Locality. Petit Key [Berry Islands], Bahamas.

Taxon 196. *Strophiops procliva* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 134, pl. 31, figs. 5, 6.** Examined 145 specimens. Size given as 1.10 by .45 [inches; 27.9 by 11.4 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 145 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 145 syntypes. Lot number MCZ 76210 contains a single specimen labeled "Holotype" that approximates the illustra-

tion and the measurements of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 144 syntypes, including MCZ 76209, become paralectotypes.

Lectotype Measurements. Length 27.6 mm, diameter (excluding lip) 10.9 mm; aperture height (including lip) 9.5 mm, aperture width (including lip and peristome) 7.9 mm.

Type Locality. Goat Key, Great Harbor, Berry Islands, Bahamas.

Taxon 197. *Strophiops jenneyi* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 134, pl. 31, figs. 9, 10.** Examined 1,131 specimens. Size given as 1.15 by .40 [inches; 30.5 by 10.2 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 1,131 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 1,131 syntypes. Lot number MCZ 76012 contains a single specimen labeled "Holotype" that approximates the illustrations and measurements of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 1,130 syntypes, including MCZ 76103 and USNM 419985 (75 specimens), become paralectotypes.

Lectotype Measurements. Length 31.1 mm, diameter (excluding lip) 11.6 mm; aperture height (including lip) 11.1 mm, aperture width (including lip and peristome) 9.3 mm.

Type Locality. Anderson's Key, Berry Islands, Bahamas.

Taxon 198. *Strophiops travellii* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 135** [as *travelii*], **pl. 32, figs. 3, 4** [as *travellii*]. Examined 3,416 specimens. Size given as 1.35 by .45 [inches; 34.3 by 11.4 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 3,416 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 3,416 syntypes. Lot number MCZ 76363 contains a single specimen labeled "Holotype" that approximates the illustration and the measurements of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 3,416 syntypes, including MCZ 76364, MCZ 118198, and USNM 419946 (200 specimens), become paralectotypes.

Lectotype Measurements. Length 33.9 mm, diameter (excluding lip) 11.9 mm; aperture height (including lip) 11.3 mm, aperture width (including lip and peristome) 9.1 mm.

Type Locality. Bridgewater Key, Berry Islands, Bahamas.

Remarks. The taxon name appeared as *S. travelii* in the heading of the original

description and *S. travellii* in the figure caption. By listing this taxon as *S. travellii* in the sales catalog, Maynard (1924b?: [3]) acted as the First Revisor of spellings [Article 24.2.4, ICZN, 1999: 30–31], fixing the spelling as *travellii.* Clench (1957: 165) listed this taxon as *S. travelii* in his catalog.

Taxon 199. *Strophiops picturata* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 135, pl. 32, figs. 7, 8.** Examined eight specimens. Size given as 1.25 by .55 [inches; 31.8 by 14.0 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the eight specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on eight syntypes. Lot number MCZ 76019 contains a single specimen labeled "Holotype" that approximates the illustration and the measurements of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining seven syntypes become paralectotypes.

Lectotype Measurements. Length 31.9 mm, diameter (excluding lip) 13.6 mm; aperture height (including lip) 11.4 mm, aperture width (including lip and peristome) 9.8 mm.

Type Locality. Cliffs on Cabbage Key, Berry Islands, Bahamas.

Taxon 200. *Strophiops lenticularia* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 135, pl. 32, figs. 9, 10.** Examined 325 specimens. Size given as 1.19 by .40 [inches; 30.2 by 10.2 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 325 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 325 syntypes. Lot number MCZ 76362 contains a single specimen labeled "Holotype" that closely approximates the illustration and less so the measurements of this taxon. It is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 324 syntypes, including MCZ 76361, become paralectotypes.

Lectotype Measurements. Length 28.0 mm, diameter (excluding lip) 10.6 mm; aperture height (including lip) 9.7 mm, aperture width (including lip and peristome) 8.3 mm.

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Figures 199–210. Taxon 199. *Strophiops picturata* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76019. Cliffs on Cabbage Key, Berry Islands, Bahamas. Taxon 200. *Strophiops lenticularia* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76362. Staniard Creek, Andros, Bahamas. Taxon 201. *Strophiops stupida* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76281. North Key, Staniard Creek, Andros, Bahamas. Taxon 202. *Strophiops columbiana* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76339. Pigeon Key, Staniard Creek, Andros, Bahamas. Taxon 203. *Strophiops carnale* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76299. West of Morgan's Bluff, Staniard Creek, Andros, Bahamas. Taxon 204. *Strophiops panda* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76269. Saddle-Back Key, Andros, Bahamas. Taxon 205.

Strophiops crescentia Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76385. Calabash Key, Andros, Bahamas. Taxon 206. *Strophiops thayeri* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76367. East end of Thompson's Key, Berry Islands, Bahamas. Taxon 207. *Strophiops sylvatica* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76371. Chub Point Key, Berry Islands, Bahamas. Taxon 208. *Strophiops ralla* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76301. Joulter Keys, Andros, Bahamas. Taxon 209. *Strophiops rosacea* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76246. West Silver Key, Nassau, New Providence Island, Bahamas. Taxon 210. *Strophiops angustocostata* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76295. Fossil on Lower Fleming, Eleuthera, Bahamas.

Type Locality. Staniard Creek, Andros, Bahamas.

Taxon 201. *Strophiops stupida* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 135, pl. 33, figs. 1, 2.** Examined 266 specimens. Size given as 1.00 by .45 [inches; 25.4 by 11.4 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 266 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 266 syntypes. Lot MCZ 76281 contained 45 specimens and was labeled "paratype." The only slip of paper in Maynard's handwriting gave the locality data but made no mention of types. Of these, a single specimen that most closely approximated the published illustrations and measurements is here designated as the lectotype (MCZ 76281) to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 44 specimens were recatalogued as MCZ 357011 and are among the 265 syntypes that become paralectotypes.

Lectotype Measurements. Length 24.9 mm, diameter (excluding lip) 10.7 mm; aperture height (including lip) 9.3 mm, aperture width (including lip and peristome) 8.1 mm.

Type Locality. North Key, Staniard Creek, Andros, Bahamas.

Taxon 202. *Strophiops columbiana* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 136, pl. 33, figs. 3, 4.** Examined 900 specimens. Size given as .92 by .40 [inches; 23.4 by 10.2 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 900 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 900 syntypes. Lot MCZ 76339 contains a single specimen labeled "Holotype" that approximates the illustration and the measurements of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 899 syntypes, including MCZ 76338 and USNM 420054 (75 specimens), become paralectotypes.

Lectotype Measurements. Length 23.3 mm, diameter (excluding lip) 10.2 mm; aperture height (including lip) 9.0 mm, aperture width (including lip and peristome) 7.5 mm.

Type Locality. Pigeon Key, Staniard Creek, Andros, Bahamas.

Taxon 203. *Strophiops carnale* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 136, pl. 33, figs. 5, 6.** Examined 266 specimens. Size given as .90 by .35 [inches; 22.9 by 8.9 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 266 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 266 syntypes. Lot number MCZ

76299 contains a single specimen labeled "Holotype" that approximates the illustration and the measurements of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 265 syntypes, including MCZ 76300, become paralectotypes.

Lectotype Measurements. Length 23.2 mm, diameter (excluding lip) 8.9 mm; aperture height (including lip) 8.8 mm, aperture width (including lip and peristome) 7.5 mm.

Type Locality. West of Morgan's Bluff, Staniard Creek, Andros, Bahamas.

Remarks. Clench (1957: 140) lists the type locality as 1 mile west of Morgan's Bluff.

Taxon 204. *Strophiops panda* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 136, pl. 33, figs. 7, 8.** Examined 72 specimens. Size given as .98 by .45 [inches; 24.9 by 11.4 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 72 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 72 syntypes. Lot number MCZ 76269 contains a single specimen labeled "Holotype" that approximates the illustration and the measurements of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 71 syntypes, including MCZ 76268, become paralectotypes.

Lectotype Measurements. Length 26.0 mm, diameter (excluding lip) 11.2 mm; aperture height (including lip) 9.8 mm, aperture width (including lip and peristome) 8.5 mm.

Type Locality. Saddle-Back Key, Andros, Bahamas.

Taxon 205. *Strophiops crescentia* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 136, pl. 33, figs. 9, 10.** Examined 240 specimens. Size given as .95 by .40 [inches; 24.1 by 10.2 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 240 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 240 syntypes. Lot number MCZ 76385 contains a single specimen labeled "Holotype" that approximates the illustration and the measurements of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 239 syntypes, including MCZ 76260, become paralectotypes.

Lectotype Measurements. Length 24.5 mm, diameter (excluding lip) 10.2 mm; aperture height (including lip) 9.4 mm, aperture width (including lip and peristome) 7.9 mm.

Type Locality. Calabash Key, Andros, Bahamas.

Taxon 206. *Strophiops thayeri* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 137**; Maynard, 1921b [July 14], pl. 34, figs. 5, 6 [as *thayerii* in figure caption]. Examined 2,876 specimens. Size given as 1.35 by .40 [inches; 34.3 by 10.2 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 2,876 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 2,876 syntypes. Lot MCZ 76367 contains a single specimen labeled "Holotype" that approximates the illustration and the measurements of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 2,875 syntypes, including MCZ 76368, USNM 420010 (50 specimens), and USNM 420092 (400 specimens), become paralectotypes.

Lectotype Measurements. Length 30.0 mm, diameter (excluding lip) 9.8 mm; aperture height (including lip) 9.7 mm, aperture width (including lip and peristome) 8.1 mm.

Type Locality. East end of Thompson's Key, Berry Islands, Bahamas.

Remarks. The taxon name appeared as *S. thayeri* in the heading of the original description and *S. thayerii* in the figure captions, which were published in a later issue than the text. This taxon was listed as *S. thayerii* in the sales catalog (Maynard, 1924b?: [3]). Clench (1957: 165) listed this taxon as *S. thayeri* in his catalog. Lot MCZ 118209 has a single specimen labeled "Paratype," from Cabbage Key, Berry Islands. This specimen was not the same species, nor is there any mention of Cabbage Key in the description of *Cerion thayeri.* This specimen is likely mislabeled and/or miscatalogued.

Taxon 207. *Strophiops sylvatica* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 137**; Maynard, 1921b [July 15], pl. 34, figs. 7, 8. Examined 1,500 specimens. Size given as 1.12 by .47 [inches; 28.4 by 11.9 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 1,500 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 1,500 syntypes. Lot MCZ 76371 contains a single specimen labeled "Holotype" that approximates the measurements and the subsequently published illustration and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 1,499 syntypes, including MCZ 76372, MCZ 118119, and USNM 420004 (100 specimens), become paralectotypes.

Lectotype Measurements. Length 27.4 mm, diameter (excluding lip) 10.7 mm; aperture height (including lip) 9.8 mm, aperture width (including lip and peristome) 8.8 mm.

Type Locality. Chub Point Key, Berry Islands, Bahamas.

Taxon 208. *Strophiops ralla* **Maynard and Clapp *in* Maynard, 1921a [May 2]: 137**; Maynard, 1921b [July 15], pl. 34, figs. 8, 9. Examined 65 specimens. Size

given as 1.20 by .47 [inches; 30.5 by 11.9 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 65 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 65 syntypes. Lot MCZ 76301 contains a single specimen labeled "Holotype" that approximates the measurements and subsequently published illustrations of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to these figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 64 syntypes, including MCZ 76302 and MCZ 118356, become paralectotypes.

Lectotype Measurements. Length 29.4 mm, diameter (excluding lip) 11.9 mm; aperture height (including lip) 10.8 mm, aperture width (including lip and peristome) 8.3 mm.

Type Locality. Joulter Keys, Andros, Bahamas.

Taxon 209. *Strophiops rosacea* **Maynard and Clapp *in* Maynard, 1921b [July 15]: 139, pl. 35, figs. 7, 8.** Examined 1,759 specimens. No measurements provided.

Type Material. The original description did not distinguish among the 1,759 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 1,759 syntypes. No specimen labeled "Holotype" was located at the MCZ, nor had any been catalogued as such in the material from Maynard's collection.

MCZ 76246 contains 159 paratypes, of which one was segregated in a vial and labeled "figured." This specimen approximates the published figure and measurements and is here designated as the lectotype to provide an objective standard of reference for this species-group taxon. The remaining 158 specimens were recatalogued as MCZ 356678, and, together with MCZ 76246, USNM 419966 (100 specimens), and USNM 420026 (100 specimens), are among the 1,758 syntypes that become paralectotypes.

Lectotype Measurements. Length 29.1 mm, diameter (excluding lip) 11.7 mm; aperture height (including lip) 10.0 mm, aperture width (including lip and peristome) 9.1 mm.

Type Locality. West Silver Key, Nassau, New Providence Island, Bahamas.

Taxon 210. *Strophiops angustocostata* **Maynard and Clapp *in* Maynard, 1921b [July 15]: 141, pl. 37, figs. 7, 8.** Examined eight specimens. Size given as 1.05 by .55 [inches; 26.7 by 14.0 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the eight specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on eight syntypes. Lot MCZ 76295 contains a single specimen labeled "Paratype" that approximates the length measurement and illustrations of this taxon and is accompanied by a label in Maynard's hand that includes references to the figures but does not contain the term

"type." This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining seven syntypes become paralectotypes.

Lectotype Measurements. Length 26.5 mm, diameter (excluding lip) 11.6 mm; aperture height (including lip) 10.5 mm, aperture width (including lip and peristome) 9.5 mm.

Type Locality. Fossil on Lower Fleming [Eleuthera, Bahamas].

Remarks. Clench (1952: 109) listed this taxon as a synonym of *Cerion exiguum* (Maynard, 1913).

Taxon 211. *Strophiops crassalabra* **Maynard and Clapp *in* Maynard, 1921b [July 15]: 143**; Maynard, 1924a [October 25], pl. 39, figs. 7, 8 [figures published with the label *S. crassamarga*]. Examined 300 specimens. Size given as 1.15 by .40 [inches; 29.2 by 10.2 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 300 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 300 syntypes. Lot MCZ 76359 contains a single specimen labeled "Holotype" that approximates the measurements and later illustrations of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 299 syntypes, including MCZ 76360 and MCZ 118274, become paralectotypes.

Lectotype Measurements. Length 28.7 mm, diameter (excluding lip) 11.3 mm; aperture height (including lip) 10.3 mm, aperture width (including lip and peristome) 8.1 mm.

Type Locality. Cliffs on east side of Rose Island, opposite Low Bay Key, New Providence Island, Bahamas.

Remarks. Misspelled as *S. crassilabra* in the sales catalog (Maynard, 1924c?: [6]). See also *Strophiops crassamarga* [Taxon 233]. Gould and Woodruff (1986: 481) reported that they had seen the "Holotype" and synonymized *Cerion crassalabra* with *C. glans* (Küster, 1844).

Taxon 212. *Strophiops angustalabra* **Maynard and Clapp *in* Maynard, 1921b [July 15]: 143–144**; Maynard, 1924a [October 25], pl. 39, figs. 9, 10. Examined 500 specimens. Size given as .95 by .45 [inches; 24.1 by 11.4 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 500 specimens examined. In the preamble to the taxonomic portion to this publication,

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Figures 211–222. Taxon 211. *Strophiops crassalabra* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76359. Cliffs on east side of Rose Island, opposite Low Bay Key, New Providence Island, Bahamas. Taxon 212. *Strophiops angustalabra* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76329. Low cliffs on west side of Rose Island, opposite Green Key, New Providence Island, Bahamas. Taxon 213. *Strophiops palidula* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76274. Extreme east end of Hog Island [Paradise Island], New Providence Island, Bahamas. Taxon 214. *Strophiops saxitina* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76326. Hog Island [Paradise Island], east of Three Bays on rock of shore, New Providence Island, Bahamas. Taxon 215. *Strophiops albata* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76258. Southern end of Rose Island, New Providence Island, Bahamas. *Strophiops vagabunda* Maynard and Clapp *in* Maynard, 1925 [Taxon 248], is a new name for *S. albata* Maynard and Clapp *in* Maynard, 1921, not *S. albata* Maynard and Clapp *in* Maynard, 1921 [Taxon 192]. Taxon 216. *Strophiops mobile* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76309. Extreme west end of Rose Island, New Providence Island, Bahamas. Taxon 217. *Strophiops hartbennetii* Maynard and Clapp *in* Maynard,

1921. Lectotype MCZ 76001. Poters Key, New Providence Island, Bahamas. Taxon 218. *Strophiops oscula* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76333. Old Thompson Place, off East Bay Street, Nassau, New Providence Island, Bahamas. Taxon 219. *Strophiops eratica* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76387. Near Fox Hill Village, New Providence Island, Bahamas. Taxon 220. *Strophiops castra* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76388. Field west of Williams Street, Nassau, New Providence Island, Bahamas. Taxon 221. *Strophiops rubiginosa* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76006. Field east of Methodist Church on Sherley Street, Nassau, New Providence Island, Bahamas. Taxon 222. *Strophiops migratoria* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76312. Grounds directly about Methodist Sunday School building, Sherley Street, Nassau, New Providence Island, Bahamas.

Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 500 syntypes. Lot number MCZ 76329 contains a single specimen labeled "Holotype" that approximates the measurements and subsequently published illustrations of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to these figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 499 syntypes, including MCZ 76328 and MCZ 118269, become paralectotypes.

Lectotype Measurements. Length 24.2 mm, diameter (excluding lip) 11.0 mm; aperture height (including lip) 10.0 mm, aperture width (including lip and peristome) 8.1 mm.

Type Locality. Low cliffs on west side of Rose Island, opposite Green Key, New Providence Island, Bahamas.

Remarks. Gould and Woodruff (1986: 481) reported that they had seen the "Holotype" and synonymized *Cerion angustalabra* with *C. glans* (Küster, 1844).

Taxon 213. *Strophiops palidula* **Maynard and Clapp *in* Maynard, 1921b [July 15]: 145**; Maynard, 1925 [July 18], pl. 40, figs. 9, 10. Examined 1,054 specimens. Size given as 1.10 by .40 [inches; 27.9 by 10.2 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 1,054 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 1,054 syntypes. Lot number MCZ 76274 contains a single specimen labeled "Holotype" that approximates the measurements and later illustrations of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 1,053 syntypes, including MCZ 76275 and USNM 419991 (250 specimens), become paralectotypes.

Lectotype Measurements. Length 27.8 mm, diameter (excluding lip) 10.7 mm; aperture height (including lip) 9.6 mm, aperture width (including lip and peristome) 7.4 mm.

Type Locality. Extreme east end of Hog Island [Paradise Island, New Providence Island, Bahamas].

Remarks. Gould and Woodruff (1986: 475) reported that they had seen the "Holotype." These authors synonymized *Strophiops palidula* with *Cerion glans* (Küster, 1844).

Taxon 214. *Strophiops saxitina* **Maynard and Clapp *in* Maynard, 1921b [July 15]: 145**; 1925 [July 18], pl. 41, figs. 1, 2. Examined 100 specimens. Size given as .76 by .35 [inches; 19.3 by 8.9 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 100 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 100 syntypes. Lot number MCZ 76326 was labeled "Holotype" but con-

tains two specimens and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. The specimen that more closely approximates the measurements and later illustrations of this taxon is here designated as the lectotype (MCZ 76326) to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The other specimen was recatalogued as MCZ 357012. It and MCZ 76327 are among the remaining 99 syntypes that become paralectotypes.

Lectotype Measurements. Length 19.4 mm, diameter (excluding lip) 9.8 mm; aperture height (including lip) 7.6 mm, aperture width (including lip and peristome) 6.3 mm.

Type Locality. Hog Island, east of Three Bays on rock of shore, New Providence Island, Bahamas.

Remarks. The plate containing the illustrations of this taxon was issued 4 years after the publication of the description. Gould and Woodruff (1986: 481) considered this taxon to be a synonym of *Cerion glans* (Küster, 1844).

Taxon 215. *Strophiops albata* **Maynard and Clapp *in* Maynard, 1921b [July 15]: 145**; Maynard and Clapp *in* Maynard, 1925 [July 18], pl. 41, figs. 7, 8 [the figures are labeled *S. vagabunda*] [junior primary homonym of *S. albata* Maynard and Clapp *in* Maynard, 1921a; *S. vagabunda* Maynard and Clapp *in* Maynard, 1925 (Taxon 248), is the next available name]. Examined 72 specimens. Size given as 1.10 by .45 [inches; 27.9 by 11.4 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 72 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 72 syntypes. Lot MCZ 76258 contains a single specimen accompanied by two MCZ labels that refer to this specimen as the holotype of *Strophiops vagabunda*, a replacement name for the preoccupied *S. albata* (see Remarks). A label in Maynard's hand contains the name *S. vagabunda* and the term "type" and includes references to the figures. This specimen is here designated as the lectotype of *S. albata* Maynard and Clapp in Maynard, 1921b, and also [Article 72: 7, ICZN, 1999: 78] its replacement name *Strophiops vagabunda* Maynard and Clapp in Maynard, 1925, to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 71 syntypes, including MCZ 76256 and MCZ 76257, become paralectotypes of *S. albata* Maynard and Clapp in Maynard, 1921b, and consequently [Article 72: 7, ICZN, 1999: 78] its replacement name *Strophiops vagabunda* Maynard and Clapp in Maynard, 1925.

Lectotype Measurements. Length 28.0 mm, diameter (excluding lip) 11.2 mm; aperture height (including lip) 10.3 mm, aperture width (including lip and peristome) 8.8 mm.

Type Locality. Southern end of Rose Island, New Providence Island, Bahamas.

Remarks. The binomen *Strophiops albata* had been previously proposed by Maynard and Clapp *in* Maynard, 1921 ([May 2]: 132–133, pl. 30, figs. 3, 4) (see Taxon 192). The second description of *S. albata* cites different measurements, a different number of specimens examined, and a different type locality and refers to an illustration of a different specimen intended to serve as the type. *Strophiops albata* Maynard and Clapp *in* Maynard, 1921b, is a junior primary homonym of *Strophiops albata* Maynard and Clapp *in* Maynard, 1921a. Maynard (1925, pl. 41, figs. 7, 8) apparently recognized the hom-

onymy and captioned the subsequently published illustrations *S. vagabunda.* As noted by Clench (1957: 166), *Strophiops vagabunda* Maynard, 1925, is a next available name for *S. albata* Maynard and Clapp *in* Maynard, 1921b, not *S. albata* Maynard and Clapp *in* Maynard, 1921a. Gould and Woodruff (1986: 474) erroneously reported *S. albata* Maynard and Clapp *in* Maynard, 1921b, to be a nomen nudum and considered *S. vagabunda* to be a synonym of *Cerion glans* (Küster, 1844).

Taxon 216. *Strophiops mobile* **Maynard and Clapp *in* Maynard, 1921b [July 15]: 146**; Maynard and Clapp *in* Maynard, 1925 [July 18], pl. 41, figs. 9, 10. Examined 61 specimens. Size given as 1.00 by .40 [inches; 25.4 by 10.2 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 61 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 61 syntypes. Lot number MCZ 76309 contains a single specimen labeled "Holotype" that approximates the measurements and later illustrations of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 60 syntypes, including MCZ 76310, become paralectotypes.

Lectotype Measurements. Length 25.8 mm, diameter (excluding lip) 10.6 mm; aperture height (including lip) 9.7 mm, aperture width (including lip and peristome) 7.8 mm.

Type Locality. Extreme west end of Rose Island, New Providence Island, Bahamas.

Remarks. The figures cited in the original description were issued 4 years later.

Taxon 217. *Strophiops hart-bennetii* Maynard, 1919b [November 6]: 36 [nomen nudum]. *Strophiops hartbennetii* **Maynard and Clapp *in* Maynard, 1921b [July 15]: 146** [as *hart-bennetii*—see Remarks]; Maynard and Clapp *in* Maynard, 1926 [March 24], pl. 42, figs. 3, 4 [as *hart-benettii*]. Examined 500 specimens. Size given as .80 by .32 [inches; 20.3 by 8.1 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 500 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 500 syntypes. Lot number MCZ 76001 contains a single specimen labeled "Holotype" that approximates the measurements and later illustrations of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 499 syntypes, including MCZ 76002, MCZ 118271, and USNM 420022 (50 specimens), become paralectotypes.

Lectotype Measurements. Length 20.9 mm, diameter (excluding lip) 8.4 mm; aperture height (including lip) 7.4 mm, aperture width (including lip and peristome) 5.7 mm.

Type Locality. Poters Key [New Providence Island, Bahamas].

Remarks. The binomen first appeared as a nomen nudum (Maynard, 1919b: 36). The taxon name is spelled *hart-bennetii* in the original description, on the handwritten label, and in the sales catalog (Maynard, 1924?: [6]). The plate, with the spelling *hart-benettii,* was issued 6 years later and is considered a subsequent misspelling. According to Article 32.5.2.4 (ICZN, 1999: 40), the taxon name is *hartbennetii* because hyphens are to be removed.

Taxon 218. *Strophiops oscula* **Maynard and Clapp *in* Maynard, 1921b [July 15]: 146**; Maynard and Clapp *in* Maynard, 1926 [March 24], pl. 42, figs. 5, 6. Examined 442 specimens. Size given as 95 by 35 [sic = .95 by .35] [inches; 24.1 by 8.9 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 442 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 442 syntypes. Lot MCZ 76333 contains a single specimen labeled "Holotype" that approximates the measurements and later illustrations of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 441 syntypes, including MCZ 76332 and USNM 420116 (100 specimens), become paralectotypes.

Lectotype Measurements. Length 23.8 mm, diameter (excluding lip) 10.0 mm; aperture height (including lip) 8.3 mm, aperture width (including lip and peristome) 7.1 mm.

Type Locality. Old Thompson Place off East Bay Street, Nassau [New Providence Island, Bahamas].

Remarks. The illustrations were issued nearly 5 years after the original description was published. Gould and Woodruff (1986: 476) regarded this taxon to be "intermediate" between *Cerion glans* (Küster, 1844) and *C. gubernatorium* (Crosse, 1869).

Taxon 219. *Strophiops eratica* **Maynard and Clapp *in* Maynard, 1921b [July 15]: 147**; Maynard and Clapp *in* Maynard, 1926 [March 24], pl. 42, figs. 7, 8. Examined 14 specimens. Size given as .90 by .35 [inches; 22.9 by 8.9 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 14 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 14 syntypes. Lot number MCZ 76387 contains a single specimen labeled "Holotype" that approximates the measurements and later illustrations of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 13 syntypes become paralectotypes.

Lectotype Measurements. Length 23.7 mm, diameter (excluding lip) 9.5 mm; aperture height (including lip) 9.1 mm, aperture width (including lip and peristome) 7.3 mm.

Type Locality. Near Fox Hill Village, New Providence Island, Bahamas.

Remarks. The illustrations were issued

nearly 5 years after the original description was published. Gould and Woodruff (1986: 477) regarded this taxon to be typical of coastal *Cerion gubernatorium* (Crosse, 1869).

Taxon 220. *Strophiops castra* **Maynard and Clapp *in* Maynard, 1921b [July 15]: 147**; Maynard and Clapp *in* Maynard, 1926 [March 24], pl. 42, figs. 9, 10. Examined 14 specimens. Size given as 1.12 by .42 [inches; 28.4 by 10.7 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 14 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 14 syntypes. Lot number MCZ 76388 contains a single specimen labeled "Holotype" that approximates the measurements and later illustrations of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 13 syntypes become paralectotypes.

Lectotype Measurements. Length 24.7 mm, diameter (excluding lip) 9.9 mm; aperture height (including lip) 8.7 mm, aperture width (including lip and peristome) 7.3 mm.

Type Locality. Field west of Williams Street, Nassau [New Providence Island, Bahamas].

Taxon 221. *Strophiops rubiginosa* **Maynard and Clapp *in* Maynard, 1921b [July 15]: 147**; Maynard and Clapp *in* Maynard, 1926 [March 24], pl. 43, figs. 1, 2. Examined 385 specimens. Size given as .85 by .28 [inches; 21.6 by 7.1 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 385 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 385 syntypes. Lot MCZ 76006 contains a single specimen labeled "Holotype" that differs substantially from the published measurements for this taxon but approximates the later illustrations and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 384 syntypes, including MCZ 76007, MCZ 356679, and USNM 420089 (50 specimens), become paralectotypes.

Lectotype Measurements. Length 27.7 mm, diameter (excluding lip) 11.3 mm; aperture height (including lip) 9.5 mm, aperture width (including lip and peristome) 7.8 mm.

Type Locality. Field east of Methodist Church on Sherley Street, Nassau [New Providence Island, Bahamas].

Remarks. The illustrations were issued nearly 5 years after the taxon description was published. Gould and Woodruff (1986: 476) regarded this taxon to be "intermediate" between *Cerion glans* (Küster, 1844) and *C. gubernatorium* (Crosse, 1869).

Taxon 222. *Strophiops migratoria* **Maynard and Clapp *in* Maynard, 1921b [July 15]: 147**; Maynard and Clapp *in* Maynard, 1926 [March 24], pl. 43, figs. 3, 4. Examined 75 specimens. Size given as 1.10 by .40 [inches; 27.9 by 10.2 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 75 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 75 syntypes. Lot number MCZ 76312 contains a single specimen labeled "Holotype" that approximates the measurements and later illustrations of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 74 syntypes, including MCZ 76311, become paralectotypes.

Lectotype Measurements. Length 27.8 mm, diameter (excluding lip) 11.2 mm; aperture height (including lip) 9.9 mm, aperture width (including lip and peristome) 8.2 mm.

Type Locality. Grounds directly about Methodist Sunday School building, Sherley Street, Nassau [New Providence Island, Bahamas].

Remarks. The illustrations were issued nearly 5 years after the original description was published. Gould and Woodruff (1986: 476) regarded this taxon to be "intermediate" between *Cerion glans* (Küster, 1844) and *C. gubernatorium* (Crosse, 1869).

Taxon 223. *Strophiops mayoi* **Maynard and Clapp *in* Maynard, 1921b [July 15]: 148**; Maynard and Clapp *in* Maynard, 1926 [March 24], pl. 43, figs. 9, 10. Examined 575 specimens. Size given as 1.03 by .40 [inches; 26.2 by 10.2 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 575 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 575 syntypes. Lot MCZ 76318 contains a single specimen labeled "Holotype" that approximates the measurements and later illustrations of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 574 syntypes, including MCZ 76317 and USNM 420025 (200 specimens), become paralectotypes.

Lectotype Measurements. Length 26.3 mm, diameter (excluding lip) 10.6 mm; aperture height (including lip) 9.3 mm, aperture width (including lip and peristome) 8.1 mm.

Type Locality. In field east of Mackey Street, Nassau [New Providence Island, Bahamas].

Remarks. The illustrations of this taxon were issued nearly 5 years after the original description was published. Gould and Woodruff (1986: 476) regarded this taxon to be "intermediate" between *Cerion glans* (Küster, 1844) and *C. gubernatorium* (Crosse, 1869).

Taxon 224. *Strophiops reincarnata* **Maynard and Clapp *in* Maynard, 1921b [July 15]: 148,** pl. 44, figs. 1, 2 [pl. 44 was never issued]. Examined 176 specimens. Size given as 1.12 by .40 [inches; 28.4 by 10.2 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 176 specimens examined. In the preamble to the taxonomic portion to this publication,

Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 176 syntypes. Lot number MCZ 76322 contains a single specimen labeled "Holotype" that approximates the measurements and later illustrations of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 175 syntypes, including MCZ 76321, become paralectotypes.

Lectotype Measurements. Length 28.5 mm, diameter (excluding lip) 10.9 mm; aperture height (including lip) 9.9 mm, aperture width (including lip and peristome) 8.2 mm.

Type Locality. Near Ocean Hole E of Mackey Street, Nassau [New Providence Island, Bahamas].

Remarks. The illustrations of this taxon were never issued. Gould and Woodruff (1986: 476) regarded this taxon to be an "anomalously located species attributable to *Cerion glans.*"

Taxon 225. *Strophiops fincastlei* **Maynard and Clapp *in* Maynard, 1921b [July 15]: 148,** pl. 44, figs. 5, 6 [pl. 44 was never issued]. Examined 150 specimens. Size given as .85 by .47 [inches; 21.6 by 11.9 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 150 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 150 syntypes. Lot number MCZ 76015 contains a single specimen labeled "Holotype" that approximates the measurements of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the unpublished figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 149 syntypes, including MCZ 76016 and MCZ 118102, become paralectotypes.

Lectotype Measurements. Length 21.7 mm, diameter (excluding lip) 9.5 mm; ap-

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Figures 223–236. Taxon 223. *Strophiops mayoi* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76318. Field east of Mackey Street, Nassau, New Providence Island, Bahamas. Taxon 224. *Strophiops reincarnata* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76322. Near Ocean Hole east of Mackey Street, Nassau, New Providence Island, Bahamas. Taxon 225. *Strophiops fincastlei* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76015. Vicinity of Fort Fincastle, West Nassau, New Providence Island, Bahamas. Taxon 226. *Strophiops novita* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76319. In park west of Fort Montague, East Nassau, New Providence Island, Bahamas. Taxon 227. *Strophiops phoenecia* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76330. Waterloo, East Nassau, New Providence Island, Bahamas. Taxon 228. *Strophiops muralia* Maynard and Clapp *in* Maynard, 1921. [Not illustrated.] Lectotype MCZ 76389. In walls at East Nassau, New Providence Island, Bahamas. Taxon 229. *Strophiops rosea* Maynard and Clapp *in* Maynard, 1921. The type of *Cerion* (*Maynardia*) *agassizii* Dall, 1894, is designated as the neotype of *Strophiops rosea* Maynard and Clapp *in* Maynard, 1921, making *Strophiops rosea* Maynard and Clapp *in* Maynard, 1921, an objective junior synonym of *Cerion* (*Maynardia*) *agassizii* Dall, 1894. Taxon 230. *Strophiops gigantea* Maynard and Clapp *in* Maynard, 1921. Holotype MCZ 76244. In wall on Village Road, near Sherley Street, Nassau, New Providence Island, Bahamas. *Strophiops ajax* Maynard, 1924 [Taxon 246], is a replacement name for this taxon, a homonym of *Strophia grayi gigantea* Maynard, 1894 [Taxon 36]. Taxon 231. *Strophiops leva* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76337. In rock above Queen's Staircase, Nassau, New Providence Island, Bahamas. Taxon 232. *Strophiops flacida* Maynard and Clapp *in* Maynard, 1921. Lectotype MCZ 76397. In rock above Queen's Staircase, Nassau,

New Providence Island, Bahamas. Taxon 233. *Strophiops crassamarga* Maynard and Clapp *in* Maynard, 1924. [Not illustrated.] *Strophiops crassamarga* has the same type specimens and type locality and is an objective junior synonym of *Strophiops crassalabra* Maynard and Clapp *in* Maynard, 1921 [Taxon 210]. Taxon 234. *Strophiops extranea* Maynard, 1924. Holotype MCZ 76142. Roseville Key, Exuma Group, Bahamas. Taxon 235. *Strophiops albicostata* Maynard and Clapp *in* Maynard, 1924. Lectotype MCZ 76109. Long Key southeast of Highburn Key, Exuma Group, Bahamas. Taxon 236. *Strophiops extensa* Maynard, 1924. Lectotype MCZ 76008. Churchyard of the Baptist Chapel on St. James St., East Nassau, New Providence Island, Bahamas.

erture height (including lip) 8.0 mm, aperture width (including lip and peristome) 6.3 mm.

Type Locality. Vicinity of Fort Fincastle, West Nassau [New Providence Island, Bahamas].

Remarks. This taxon was never illustrated. In the original description, Maynard noted that many of the 150 specimens were dead and later (1924c: 6) listed *S. fincastlei* as extinct in 1924 because of the burning of vegetation prior to cultivation. Gould and Woodruff (1986: 476) regarded this taxon to be "intermediate" between *Cerion glans* (Küster, 1844) and *C. gubernatorium* (Crosse, 1869).

Taxon 226. *Strophiops novita* Maynard, 1919b [November 6]: 36 [nomen nudum]; **Maynard and Clapp *in* Maynard, 1921b [July 15]: 148,** pl. 45, figs. 1, 2 [pl. 45 was never issued]. Examined 251 specimens. Size given as .90 by .35 [inches; 22.9 by 8.9 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 251 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 251 syntypes. Lot MCZ 76319 contains a single specimen labeled "Holotype" that approximates the measurements of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the unpublished figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 250 syntypes, including MCZ 118104, become paralectotypes.

Lectotype Measurements. Length 23.0 mm, diameter (excluding lip) 9.2 mm; aperture height (including lip) 8.6 mm, aperture width (including lip and peristome) 6.9 mm.

Type Locality. In park west of Fort Montague, East Nassau [New Providence Island, Bahamas].

Remarks. This taxon, which first appeared as a nomen nudum (Maynard, 1919b: 36), was never illustrated. Maynard (1924c: 6) listed *S. novita* as nearly extinct (only one specimen) in 1924 from the burning of vegetation prior to cultivation. Gould and Woodruff (1986: 476) regarded this taxon to be "intermediate" between *Cerion glans* (Küster, 1844) and *C. gubernatorium* (Crosse, 1869).

Taxon 227. *Strophiops phoenicia* Maynard, 1919b [November 6]: 36 [nomen nudum]. *S. phoenecia* **Maynard and Clapp *in* Maynard, 1921b [July 15]: 149, pl. 45, figs. 3, 4** [pl. 45 was never issued]; Maynard, 1924b?: [4]; Maynard, 1924c: 6. Examined 1,550 specimens. Size given as .85 by .33 [inches; 21.6 by 8.4 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 1,550 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 1,550 syntypes. Lot MCZ 76330 contains a single specimen labeled "Holotype" that approximates the measurements and later illustrations of this taxon and is accompanied by a label in Maynard's hand with the term "type," which includes references to the figures. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original con-

cept of it. The remaining 1,549 syntypes, including MCZ 76331, MCZ 118156, and USNM 420059 (50 specimens), become paralectotypes.

Lectotype Measurements. Length 22.2 mm, diameter (excluding lip) 8.6 mm; aperture height (including lip) 7.9 mm, aperture width (including lip and peristome) 6.2 mm.

Type Locality. Waterloo, East Nassau, New Providence Island, Bahamas.

Remarks. The binomen *S. phoenicea* first appeared as a nomen nudum (Maynard, 1919b: 36). The taxon description used the spelling *S. phoenecia,* as did the sales catalog (Maynard, 1924b?: [4]). Maynard (1924c: 6) listed *S. phoenecia* as extinct in 1924 from the burning of vegetation prior to cultivation. Gould and Woodruff (1986: 477) regarded this taxon to be a synonym of *Cerion gubernatorium* (Crosse, 1869).

Taxon 228. *Strophiops muralia* **Maynard and Clapp *in* Maynard, 1921b [July 15]: 151,** pl. 47, figs. 5, 6 [pl. 47 was never issued]. Examined 4 specimens. Size given as 1.05 by .45 [inches; 26.7 by 11.4 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the four specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on four syntypes. Lot MCZ 76389 contains a single specimen labeled "Holotype" that approximates the measurements and later illustrations of this taxon and is accompanied by a label in Maynard's hand with the term "type." This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining three syntypes become paralectotypes.

Lectotype Measurements. Length 26.4 mm, diameter (excluding lip) 12.1 mm; aperture height (including lip) 10.5 mm, aperture width (including lip and peristome) 8.9 mm.

Type Locality. In walls at East Nassau, New Providence Island, Bahamas.

Remarks. Gould and Woodruff (1986: 481) examined the "Holotype" of this taxon and attributed it to the synonymy of *Cerion agassizii* Dall, 1894.

Taxon 229. *Strophiops rosea* **Maynard and Clapp *in* Maynard, 1921b [July 15]: 151,** pl. 48, figs. 9, 10 [pl. 48 was never issued]. Examined one specimen. Size given as .73 by .36 [inches; 18.5 by 9.1 mm], but the term "type" was not used.

Type Material. The original description was based on a single specimen, the unique holotype, for which measurements were provided but for which the illustrations were never published. The specimen was not at the MCZ, nor was there any catalog entry for this taxon at the MCZ at the time Maynard's collection was catalogued. Searches of the collections and/or databases of the USNM, the Academy of Natural Sciences of Philadelphia, the Field Museum of Natural History, the Florida Museum of Natural History, and the Museum of Biological Diversity, Ohio State University, failed to uncover a single specimen catalogued under this name. Maynard's original brief description—"Similar to last [*S. agassizii* Dall] but smaller, .73 by .36, with 8 instead of 11 whorls, and is tinged with dull orange"—is inadequate to differentiate this taxon from *S. agassizii* unambiguously. The holotype of *Cerion* (*Maynardia*) *agassizii* Dall, 1894 (MCZ IP 113595, Invertebrate Paleontology Collection), is here designated as the neotype of *Strophiops rosea* Maynard and Clapp *in* Maynard, 1921, to provide an objective

standard of reference for this species-group taxon. *Strophiops rosea* Maynard and Clapp *in* Maynard, 1921, becomes a junior objective synonym of *Cerion* (*Maynardia*) *agassizii* Dall, 1894.

Type Locality. Strophiops rosea was initially described as being from the northeast end of Rose Island, New Providence Island, Bahamas (Maynard and Clapp *in* Maynard, 1921: 151). According to Article 76.3 (ICZN, 1999: 87), the type locality of *Cerion agassizii* Dall, 1894, "The calcareous sand-rock at the W. quarry, top of Nassau Ridge" [New Providence Island, Bahamas], becomes the type locality of *Strophiops rosea.*

Remarks. The illustrations of this taxon were never published. Gould and Woodruff (1986: 481) mentioned that they had not seen the unique holotype of this taxon but considered it to be a "fairly unambiguous" synonym of *Cerion agassizii* Dall, 1894, on the basis of the limited description.

Taxon 230. *Strophiops gigantea* **Maynard and Clapp *in* Maynard, 1921b [July 15]: 152,** pl. 47, figs. 9, 10 [pl. 47 never issued]. Examined one specimen. Size given as 1.75 by .65 [inches; 44.5 by 16.5 mm], but the term "type" was not used.

Type Material. The original description is based on a single specimen, the unique holotype, for which measurements were provided, but for which the illustrations were never issued. Lot MCZ 76244 contains a single specimen accompanied by two MCZ labels that refer to this specimen as the holotype of *Strophiops ajax,* a replacement name for the preoccupied *S. gigantea* (see Remarks). A handwritten label with the specimen contains the name *Strophiops gigantea,* with "*gigantea*" partially erased and overwritten "*ajax.*" This specimen is the holotype both of *S. gigantea* and of *S. ajax.*

Holotype Measurements. Length 43.9 mm, diameter (excluding lip) 17.4 mm; aperture height (including lip) 17.1 mm, aperture width (including lip and peristome) 13.6 mm.

Type Locality. In wall on Village Road, near Sherley Street, Nassau, New Providence Island, Bahamas.

Remarks. Strophiops gigantea Maynard and Clapp *in* Maynard, 1921, is a homonym of *Strophia grayi gigantea* Maynard, 1894 [Taxon 36]. *Strophiops ajax* Maynard, 1924 [Taxon 246], was proposed as a replacement name. Gould and Woodruff (1986: 480) attributed this fossil taxon to *Cerion agassizii* Dall, 1894.

Taxon 231. *Strophiops leva* **Maynard and Clapp *in* Maynard, 1921b [July 15]: 152,** pl. 48, figs. 1, 2 [pl. 48 was never issued]. Examined 12 specimens. Size given as 1.10 by .50 [inches; 27.9 by 12.7 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 12 specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 12 syntypes. Lot number MCZ 76337 was labeled "Paratype" and contains 93 specimens, most damaged or incomplete, of which one was sequestered. The labels make no mention of the term "type," nor is there a reference to plates or figures. The sequestered specimen, which is complete and well preserved and had been carefully cleaned of matrix, is likely the specimen used by Maynard to prepare the species description. This specimen is here selected as the lectotype (MCZ 76337). The remaining specimens were recatalogued as MCZ 357013. The original description referred to 12 specimens, indicating that Maynard had added at least 81 specimens since the species was described. It is unclear which 11 of the remaining 92 specimens are paralectotypes.

Lectotype Measurements. Length 29.6 mm, diameter (excluding lip) 12.7 mm; aperture height (including lip) 11.5 mm, aperture width (including lip and peristome) 9.0 mm.

Type Locality. In rock above Queen's Staircase, Nassau, New Providence Island, Bahamas.

Taxon 232. *Strophiops flacida* **Maynard and Clapp *in* Maynard, 1921b [July 15]: 152,** pl. 48, figs. 3, 4 [pl. 48 was never issued]. Examined two specimens. Size given as .98 by .34 [inches; 24.9 by 8.6 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the two specimens examined. In the preamble to the taxonomic portion to this publication, Maynard (1919b: 43–44) specified that types were selected. However, there was no indication in this or any of Maynard's publications to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on two syntypes. Lot number MCZ 76397 contains a single specimen labeled "Holotype" that roughly approximates the published length of this taxon and is accompanied by a label in Maynard's hand with the term "type" that refers to the unpublished illustrations. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The other syntype (MCZ 76398) becomes a paralectotype.

Lectotype Measurements. Length 25.4 mm, diameter (excluding lip) 10.9 mm; aperture height (including lip) 10.1 mm, aperture width (including lip and peristome) 8.7 mm.

Type Locality. In rock above Queen's Staircase, Nassau, New Providence Island, Bahamas.

Remarks. Gould and Woodruff (1986: 481) regarded *S. flacida* to be a "ribby version" of *Cerion agassizii* Dall, 1894.

Taxon 233. *Strophiops crassamarga* **Maynard and Clapp *in* Maynard, 1924a [October 25], pl. 39, figs. 7, 8.**

Nomenclatural Remarks. The binomen *S. crassamarga* was published in the caption beneath the figures (pl. 39, figs. 7, 8) cited in the original description of *Strophiops crassalabra* Maynard and Clapp *in* Maynard, 1921b (p. 143), and was not used subsequently by Maynard, who listed the taxon as *S. crassilabra* in the sales catalog (Maynard, 1924b?: [6]). The specimen labeled *Strophiops crassamarga* on plate 39 (figs. 7, 8) is the lectotype of *Strophiops crassalabra* [Taxon 211], making *Strophiops crassamarga* Maynard and Clapp *in* Maynard, 1924, a junior objective synonym of *Strophiops crassalabra* Maynard and Clapp *in* Maynard, 1921.

Taxon 234. *Strophiops extranea* **Maynard, 1924c [10 December]: 2** [not illustrated]. Examined one specimen. Size given as 1.17 by .50 [inches; 29.7 by 12.7 mm], but the term "type" was not used.

Type Material. The original description stated that this taxon was based on a single fossil found embedded in rock and provided its measurements. This taxon is thus based on a unique holotype. Lot MCZ 76142 contains a single specimen labeled "Holotype" that corresponds closely to the published measurements and is here considered to be the holotype.

Holotype Measurements. Length 29.9 mm, diameter (excluding lip) 12.7 mm; aperture height (including lip) 10.8 mm, aperture width (including lip and peristome) 9.2 mm.

Type Locality. Roseville Key, Exuma Group [Bahamas].

Taxon 235. *Strophiops albicostata* Maynard and Clapp *in* Maynard, 1924b?: [3] [nomen nudum]; **Maynard, 1924c [10 December]: 2** [not illustrated]. Examined 1,000 specimens. Size given as 1.36 by .48 [inches; 34.5 by 12.2 mm], but the term "type" was not used.

Nomenclatural Remarks. Strophiops albicostata was listed for sale in Maynard's (1924b?: [3]) catalog, whereas the description of this taxon was published in the supplement to this catalog. On page [2] of the catalog, Maynard noted that, "Unless otherwise designated, all species should be accredited to Maynard and Clapp." Thus, *Strophiops albicostata* Maynard and Clapp *in* Maynard (1924b?) is a nomen nudum. The taxon became available as *Strophiops albicostata* Maynard on December 10, 1924.

Type Material. The original description did not distinguish among the 1,000 specimens examined. There was no indication in this publication to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 1,000 syntypes. Lot MCZ 76109 contains a single specimen labeled "Holotype." This specimen approximates the measurements in the original description and is here designated as the lectotype to provide an objective standard of reference for this species-group taxon. All other syntypes, including, MCZ 76110 and USNM 420061 (100 specimens), become paralectotypes.

Lectotype Measurements. Length 34.1 mm, diameter (excluding lip) 12.9 mm; aperture height (including lip) 11.64 mm, aperture width (including lip and peristome) 9.4 mm.

Type Locality. Long Key southeast of Highburn Key [Exuma Group, Bahamas].

Taxon 236. *Strophiops extensa* **Maynard, 1924c [10 December]: 2, 3** [not illustrated]. Examined 23,000 specimens. No measurements provided.

Type Material. The original description did not distinguish among the 23,000 specimens examined. There was no indication in this publication to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 23,000 syntypes. An examination of the MCZ catalog revealed that there was no specimen segregated as type for this species in Maynard's collection at the time of his death. Lot MCZ 76008 contains 278 specimens labeled "paratypes." Because this species had not been figured, nor have any measurements been published to help select the lectotype, an intact, adult, live-collected specimen that conforms to the brief description is here designated as the lectotype (MCZ 76008) to provide an objective standard of reference for this species-group taxon. The remaining 277 specimens were recatalogued as MCZ 352331. These and all other syntypes, including USNM 419996 (1,500 specimens), become paralectotypes.

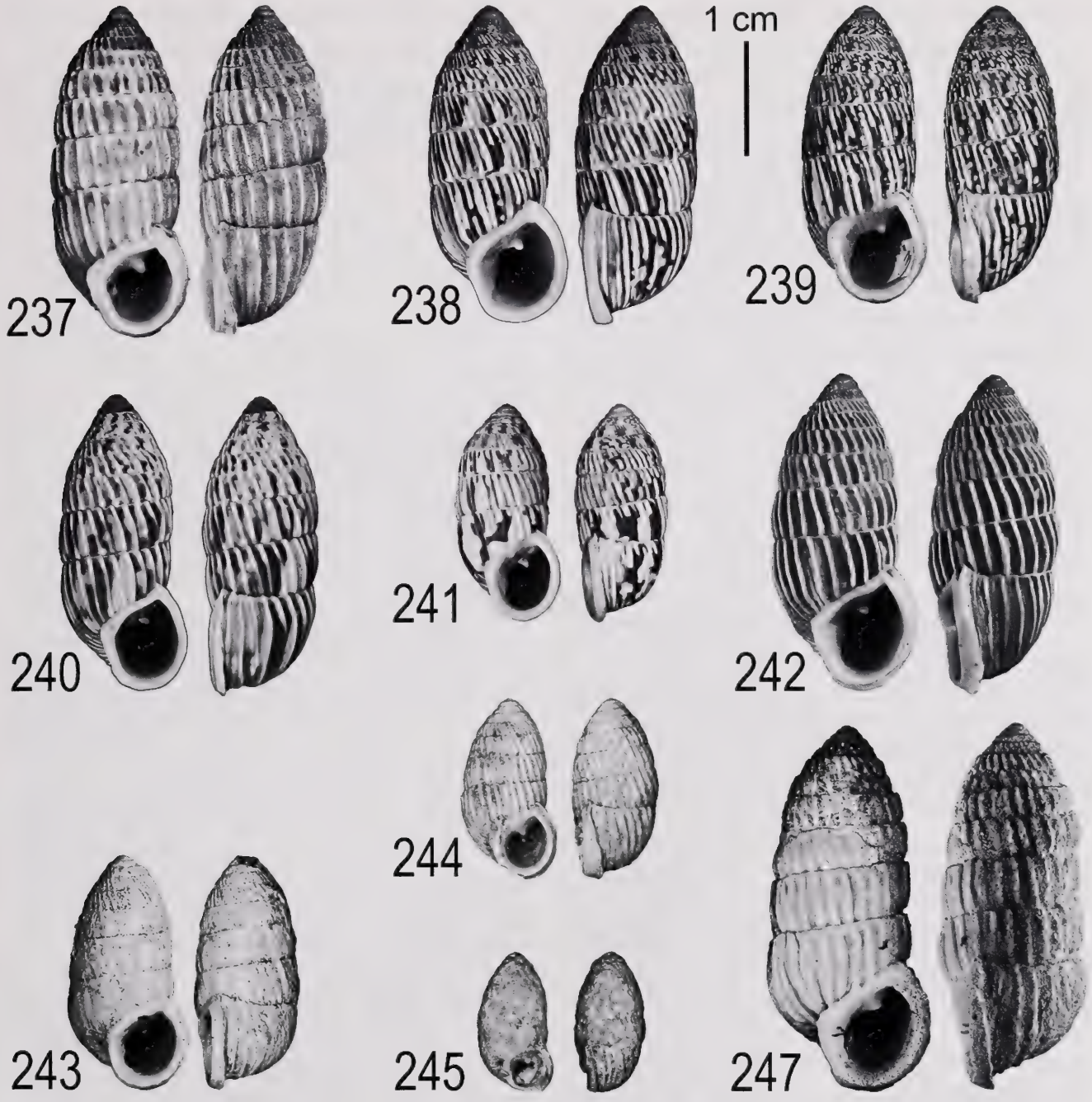
Lectotype Measurements. Length 31.5 mm, diameter (excluding lip) 10.1 mm; aperture height (including lip) 9.8 mm, aperture width (including lip and peristome) 7.9 mm.

Type Locality. Churchyard of the Baptist Chapel on St. James Street, East Nassau, New Providence Island, Bahamas.

Remarks. Maynard (1924c: 2–3) reported this taxon to be "abundant living in the church-yard of the Baptist Chapel on St. James St. East Nassau, on the west and south side of this street to Kemp's Road, but, except about the chapel, many were dead. 23,000 were collected. But out of this number only about 3000 were living." Because the lectotype was a live-collected specimen, the type locality is here restricted to the church-yard. Gould and Woodruff (1986: 476) regarded this taxon to be "intermediate" between *Cerion glans* (Küster, 1844) and *C. gubernatorium* (Crosse, 1869).

Taxon 237. *Strophiops sparsa* **Maynard, 1924c [10 December]: 3** [not illustrated]. Examined "about 280" specimens. Size given as 1.16 by .45 [inches; 29.5 by 11.4 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the "about 280"



Figures 237–248. Taxon 237. *Strophiops sparsa* Maynard, 1924. Lectotype MCZ 76399. Field at St. James Corner, East Nassau, New Providence Island, Bahamas. Taxon 238. *Strophiops rufula* Maynard, 1924. Lectotype USNM 420135. West side of Kemp's Road near the terminus of St. James St. and south of that street to St. James Corner, Nassau, New Providence Island, Bahamas. Taxon 239. *Strophiops gracila* Maynard, 1924. Lectotype MCZ 76285. Found in and near a cutting through rocks on Soldier's Road about a mile and a half from South Shore, New Providence Island, Bahamas. Taxon 240. *Strophiops montana* Maynard, 1924. Lectotype USNM 420103. Sunnyside Estate East Bay St. near the house, Nassau, New Providence Island, Bahamas. Taxon 241. *Strophiops clara* Maynard, 1924. Lectotype MCZ 76111. Church on the road to Fox Hill from East Bay St., Nassau, New Providence Island, Bahamas. Taxon 242. *Strophiops livida* Maynard, 1924. Lectotype MCZ 76101. On West Bay Street, Nassau, about opposite North Silver Key, New Providence Island, Bahamas. Taxon 243. *Strophiops minima* Maynard, 1924. Lectotype MCZ 76022. St. James Corner, East Nassau, New Providence Island, Bahamas. Taxon 244. *Strophiops concina* Maynard, 1924. Holotype MCZ 76020. St. James Corner, East Nassau, New Providence Island, Bahamas. Taxon 245. *Strophiops pygmea* Maynard, 1924. Holotype MCZ 76021. St. James Corner, East Nassau, New Providence Island, Bahamas. Taxon 246. *Strophiops ajax* Maynard, 1924. [Not illustrated.] Replacement name for *Strophiops gigantea* Maynard and Clapp *in* Maynard, 1921 [Taxon 230], not *Strophia grayi gigantea* Maynard, 1894 [Taxon 36]. The type specimens and type locality of *S. gigantea* Maynard and Clapp *in* Maynard, 1921 are also the type specimens of *S. ajax* Maynard, 1924. Taxon 247. *Strophiops leucophera* Maynard and Clapp *in* Maynard, 1925. Lectotype MCZ 76283. Gray hill at the extreme northern end of Great Guana Key, Exuma Group, Bahamas. Taxon 248. *Strophiops vagabunda* Maynard, 1925. [Not illustrated.] Replacement name for *S. albata* Maynard and Clapp *in* Maynard, 1921b [Taxon 215], not *S. albata* Maynard and Clapp *in* Maynard, 1921 [Taxon 192]. The type specimens and type locality of *Strophiops albata* Maynard and Clapp *in* Maynard, 1921 (see Taxon 214), are also the type specimens of *S. vagabunda* Maynard, 1925.

specimens examined. There was no indication in this publication to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on "about 280" syntypes. An examination of the MCZ catalog revealed that there was no specimen segregated as type for this species in Maynard's collection at the time of his death. Lot MCZ 76399 was labeled "Paratype" and contained 174 specimens. As this species had not been figured, an intact, adult, live-collected specimen from this lot that most closely approximates the published measurements and conforms to the brief description is here designated as the lectotype (MCZ 76399) to provide an objective standard of reference for this species-group taxon. The remaining 173 specimens, which were recatalogued as MCZ 357014, are among the "about 280" syntypes that become paralectotypes.

Lectotype Measurements. Length 29.3 mm, diameter (excluding lip) 11.4 mm; aperture height (including lip) 10.4 mm, aperture width (including lip and peristome) 8.9 mm.

Type Locality. Field at St. James Corner, East Nassau [New Providence Island, Bahamas].

Remarks. Maynard (1924c: 3) reported 20 specimens found living in a field at St. James Corner, East Nassau, and about 260 found dead scattered in fields from this point east to the estate called Sunnyside, but chiefly as shells occupied by hermit crabs. Because the lectotype was collected living (as evidenced by vestiges of an epiphragm around the aperture), the type locality is restricted to the field at St. James Corner, East Nassau, New Providence Island, Bahamas.

Gould and Woodruff (1986: 476) regarded this taxon to be an "anomalously located species attributable to *Cerion glans.*"

Taxon 238. *Strophiops rufula* **Maynard, 1924c [10 December]: 3** [not illustrated]. Examined 3,439 specimens. Measurements not provided.

Type Material. The original description did not distinguish among the 3,439 specimens examined. There was no indication in this publication to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 3,439 syntypes. An examination of the MCZ catalog revealed that there was no specimen segregated as type for this species in Maynard's collection at the time of his death. Large syntype lots are present in the USNM and MCZ collections. Because this species was never figured, nor had any measurements been published to help select the lectotype, an intact, adult, live-collected specimen that conforms to the brief description is here designated as the lectotype (USNM 420135) to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of this taxon. The remaining syntypes, including MCZ 76098 and USNM 1093796, become paralectotypes.

Lectotype Measurements. Lot USNM 420135, length 28.3 mm, diameter (excluding lip) 10.7 mm; aperture height (including lip) 10.9 mm, aperture width (including lip and peristome) 8.8 mm.

Type Locality. On the west side of Kemp's Road, near the terminus of St. James St. [Street] and south of that street to St. James Corner, Nassau, New Providence Island, Bahamas.

Remarks. Maynard (1924c: 3) noted that of the 3,439 specimens collected, only 649 were living.

Taxon 239. *Strophiops gracila* **Maynard, 1924c [10 December]: 3** [not illustrated]. Examined 61 specimens. Only diameter given as .40 [inches; 10.2 mm].

Type Material. The original description did not distinguish among the 61 specimens examined. There was no indication in this publication to associate a single specimen with the term "type." Thus,

there is no holotype for this taxon, and the species is based on 61 syntypes. An examination of the MCZ catalog revealed that there was no specimen segregated as type for this species in Maynard's collection at the time of his death. Lot MCZ 76285 was labeled "Paratypes" and contained 33 specimens. Because this species was never illustrated and only a measurement for the diameter was published, an intact, adult, live-collected specimen from this lot that most closely approximates the published diameter and conforms to the brief description is here designated as the lectotype to provide an objective standard of reference for this species-group taxon. The remaining 32 specimens, which were recatalogued as MCZ 357015, are among the 60 syntypes that become paralectotypes.

Lectotype Measurements. Length 26.5 mm, diameter (excluding lip) 10.2 mm; aperture height (including lip) 10.4 mm, aperture width (including lip and peristome) 8.8 mm.

Type Locality. Found in and near a cutting through rocks on Soldier's Road about a mile and a half from South Shore, New Providence Island, Bahamas.

Remarks. Gould and Woodruff (1986: 478) regarded this taxon to be a synonym of *Cerion gubernatorium* (Crosse, 1869).

Taxon 240. *Strophiops montana* **Maynard, 1924c [10 December]: 3, 4** [not illustrated]. Examined 1,219 specimens. Only diameter given as .35 [inches; 8.9 mm].

Type Material. The original description did not distinguish among the 1,219 specimens examined. There was no indication in this publication to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 1,219 syntypes. An examination of the MCZ catalog revealed that there was no specimen segregated as type for this species in Maynard's collection at the time of his death. Large syntype lots are present in the USNM and MCZ collections. Because this species had not been figured and only the diameter was published, an intact, adult, live-collected specimen that conforms to the brief description is here designated as the lectotype (USNM 420103) to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of this taxon. The remaining syntypes, including MCZ 76113 and USNM 1093794, become paralectotypes.

Lectotype Measurements. Number USNM 420103, length 26.4 mm, diameter (excluding lip) 9.8 mm; aperture height (including lip) 9.4 mm, aperture width (including lip and peristome) 7.4 mm.

Type Locality. Occurs on Sunnyside Estate East Bay St. near the house, Nassau, New Providence Island, Bahamas.

Remarks. Maynard (1924c: 3–4) noted that of the 1,219 specimens collected, only 33 were living. Gould and Woodruff (1986: 478) reported that they did not examine specimens of this taxon but regarded it to be a synonym of *Cerion gubernatorium* (Crosse, 1869).

Taxon 241. *Strophiops clara* **Maynard, 1924c [10 December]: 4** [not illustrated]. Examined four specimens. Size given as .80 by .35 [inches; 20.3 by 8.9 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the four specimens examined. There was no indication in this publication to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on four syntypes. Lot MCZ 76111 contains a single specimen labeled "Holotype" that roughly approximates the published measurements for this taxon. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon. The remaining three specimens become paralectotypes.

Lectotype Measurements. Length 19.2 mm, diameter (excluding lip) 8.3 mm; aperture height (including lip) 7.8 mm, aperture width (including lip and peristome) 6.5 mm.

Type Locality. About a church on the road to Fox Hill from East Bay St., Nassau, New Providence Island, Bahamas.

Remarks. Gould and Woodruff (1986: 477) considered this taxon to be a synonym of *Cerion gubernatorium* (Crosse, 1869).

Taxon 242. *Strophiops livida* **Maynard, 1924c [10 December]: 4** [not illustrated]. Examined 795 specimens. Measurements not provided.

Type Material. The original description did not distinguish among the 795 specimens examined. There was no indication in this publication to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 795 syntypes. Neither measurements nor illustration are included in the original description. Lot MCZ 76101 contains a single specimen labeled "Holotype" that is accompanied by a label in Maynard's hand with the term "type," which is dated July 27, 1924, presumably the date it was collected. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 794 specimens, including, MCZ 76102 and USNM 420104 (200 specimens including one sinistral), become paralectotypes.

Lectotype Measurements. Length 28.5 mm, diameter (excluding lip) 11.5 mm; aperture height (including lip) 11.7 mm, aperture width (including lip and peristome) 9.7 mm.

Type Locality. On West Bay Street, Nassau, about opposite North Silver Key, New Providence Island, Bahamas.

Remarks. Gould and Woodruff (1986: 477) considered this taxon to be a synonym of *Cerion glans* (Küster, 1844).

Taxon 243. *Strophiops minima* **Maynard, 1924c [10 December]: 4** [not illustrated]. Examined 4 specimens. Size given as .75 by .31 [inches; 19.1 by 7.9 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the four specimens examined. There was no indication in this publication to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on four syntypes. An examination of the MCZ catalog revealed that there was no specimen segregated as type for this species in Maynard's collection at the time of his death. Lot MCZ 76022 was labeled "Paratype" and contained three specimens [MCZ catalog lists five], all damaged to some degree. The best preserved specimen (lacking a portion of the protoconch) is here selected as the lectotype (MCZ 76022) to provide an objective standard of reference for this species-group taxon. The remaining two specimens, recatalogued as MCZ 357016, become paralectotypes.

Lectotype Measurements. Length 21.0 mm, diameter (excluding lip) 9.6 mm; aperture height (including lip) 8.9 mm, aperture width (including lip and peristome) 7.4 mm.

Type Locality. St. James Corner, East Nassau [New Providence Island, Bahamas].

Remarks. From crab hole, with *S. concina* and *S. pygmea.* Gould and Woodruff (1986: 482) considered this taxon to be a synonym of *Cerion gubernatorium* (Crosse, 1869), but questioned whether it were truly "fossil" or just long dead.

Taxon 244. *Strophiops concina* **Maynard, 1924c [10 December]: 4** [not illustrated]. Examined one specimen. Size given as .65 by .30 [inches; 16.5 by 7.6 mm], but the term "type" was not used.

Type Material. The original description states that this taxon is known from one specimen, the measurements provided ap-

plying to the unique holotype (MCZ 76020).

Holotype Measurements. Length 16.0 mm, diameter (excluding lip) 7.7 mm; aperture height (including lip) 6.6 mm, aperture width (including lip and peristome) 6.1 mm.

Type Locality. St. James Corner, East Nassau [New Providence Island, Bahamas].

Remarks. From crab hole, with *S. minima* and *S. pygmea.* Gould and Woodruff (1986: 481) considered this taxon to be a synonym of *Cerion universum* (Maynard, 1913).

Taxon 245. *Strophiops pygmea* **Maynard, 1924c [10 December]: 4, 5** [not illustrated]. Examined one specimen. Size given as .50 by .25 [inches; 12.7 by 6.4 mm], but the term "type" was not used.

Type Material. The original description states that this taxon is known from one specimen, the measurements provided applying to the unique holotype (MCZ 76021).

Holotype Measurements. Length 12.2 mm, diameter (excluding lip) 6.1 mm; aperture height (including lip) 4.5 mm, aperture width (including lip and peristome) 4.6 mm.

Type Locality. St. James Corner, East Nassau [New Providence Island, Bahamas].

Remarks. From crab hole, with *S. minima* and *S. concina.* Maynard (1924c: 4) noted that this was the smallest fossil Cerion known to him. Gould and Woodruff (1985: 481) considered this a synonym of *Cerion universum* (Maynard, 1913).

Taxon 246. *Strophiops ajax* **Maynard, 1924c [10 December]: 5.** Replacement name for *Strophiops gigantea* Maynard and Clapp *in* Maynard, 1921 [Taxon 230], not *Strophia grayi gigantea* Maynard, 1894 [Taxon 36].

Type Material. The type specimen (Holotype, MCZ 76244) and type locality of *S. gigantea* Maynard and Clapp, 1921 (see Taxon 230), are also the type specimen and type locality of *S. ajax* Maynard, 1924.

Taxon 247. *Strophiops leucophera* **Maynard, 1925 [July 18]: 181,** pl. 52, figs. 1, 2 (pl. 52 never published). Examined 50 specimens. Size given as .50 by 1.50 [inches; 12.7 by 38.1 mm], but the term "type" was not used.

Type Material. The original description did not distinguish among the 50 specimens examined. There was no indication in this publication to associate a single specimen with the term "type." Thus, there is no holotype for this taxon, and the species is based on 50 syntypes. Lot number MCZ 76283 contains a single specimen labeled "Holotype" that is accompanied by a label in Maynard's hand with the term "type," which includes references to figures that were never published. This specimen is here designated as the lectotype to provide an objective standard of reference for this species-group taxon that is consistent with Maynard's original concept of it. The remaining 49 specimens become paralectotypes.

Lectotype Measurements. Length 32.5 mm, diameter (excluding lip) 13.1 mm; aperture height (including lip) 12.0 mm, aperture width (including lip and peristome) 10.2 mm.

Type Locality. Gray hill at the extreme northern end of Great Guana Key, Exuma Group, Bahamas.

Remarks. The published measurements are transposed. Because this taxon was published in "Part Three" of *Contributions to the History of the Cerionidae,* the authorship is attributed to Maynard, rather than Maynard and Clapp, as listed in Clench (1957: 151).

Taxon 248. *Strophiops vagabunda* **Maynard, 1925 [July 18], pl. 41, figs. 7, 8** [appears in figure caption only].

Nomenclatural Remarks. The binomen *Strophiops vagabunda* appeared under fig-

ures cited in the original description of *Strophiops albata* Maynard and Clapp *in* Maynard, 1921b (see Taxon 215), but published 4 years later. *Strophiops albata* Maynard and Clapp *in* Maynard, 1921b, is a junior homonym of *S. albata* Maynard and Clapp *in* Maynard, 1921a (see Taxon 192). Clench (1957: 166) regarded *Strophiops vagabunda* to be a replacement name for *S. albata* Maynard and Clapp *in* Maynard, 1921b, not *S. albata* Maynard and Clapp *in* Maynard, 1921a, but attributed authorship to Maynard and Clapp. As the figures are captioned "*S. vagabunda*" authorship of the taxon is confined to Maynard, 1925.

Type Material. The type specimens (Lectotype, MCZ 76258) and type locality of *Strophiops albata* Maynard and Clapp *in* Maynard, 1921 (see Taxon 215), are also the type specimens and type locality of *S. vagabunda* Maynard, 1925.

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